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TABLE OF CONTENTS

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SPADELLA GAETANOI, A NEW BENTHIC CHAETOGNATH FROM HAWAII

Angeles Alvariño

Abstract.—The new *Spadella* is described and compared with the related species *S. cephaloptera*, *S. angulata* and *S. bradshawi*, with which it agrees in the lack of adhesive digital organs. The diagnostic characteristics of *S. gaetanoi* and the three closely related species of *Spadella* are compiled (Table 1). Information on the habitat and the food of *S. gaetanoi* is also included.

The genus *Spadella* Langerhans was discussed by Alvariño (1970), who compiled the diagnostic characteristics and world distribution of the species. Since that time, another species of *Spadella*, *S. bradshawi* Bieri, 1974, has been described from California. The new species described herein is related to *S. cephaloptera*, *S. angulata* and *S. bradshawi*, with which it agrees in several characteristics, such as lack of adhesive digital organs. However, *S. cephaloptera* and *S. angulata* have intestinal diverticula, which are absent in *S. bradshawi* and *Spadella* new species.

Spadella gaetanoi, new species
Figs. 1–2

Material.—Holotype (USNM 55361) and 6 paratypes (USNM 55362) collected at Kure Atoll (Hawaii) in August 1977.

Diagnosis.—The body is opaque, flattened dorso-ventrally and with well developed muscles (Fig. 1A, B). Total length when mature, 2–3 mm, tail fin not included. The body is widest at the posterior part of the trunk. The head is large, roundish, almost twice as wide as the neck. Neck is distinct, and covered by a thick collarette (Fig. 2A). The caudal segment constitutes 53–55% of the total length. The eyes are large, round; the pigmented region is large, and the pigment is in an H shape, leaving 4 clear spaces filled by lenses. The hooks are slender, rather strongly curved, usually 8 or 9 (up to 10) at each side of the head. The anterior teeth are 4 per set at each side of the head. They are long, thin and curved. The teeth at the middle of each set are the longest. The posterior teeth are 4 or 5 at each side of the head. They are thin and small, when present. The corona ciliata is a perfect oval, not as thick as in *S. bradshawi*, with the longest axis transverse to the longitudinal axis of the body. It covers the neck, extending into the collarette region of the neck. The collarette is thick, well developed, extending from the head to the level of the posterior septum and

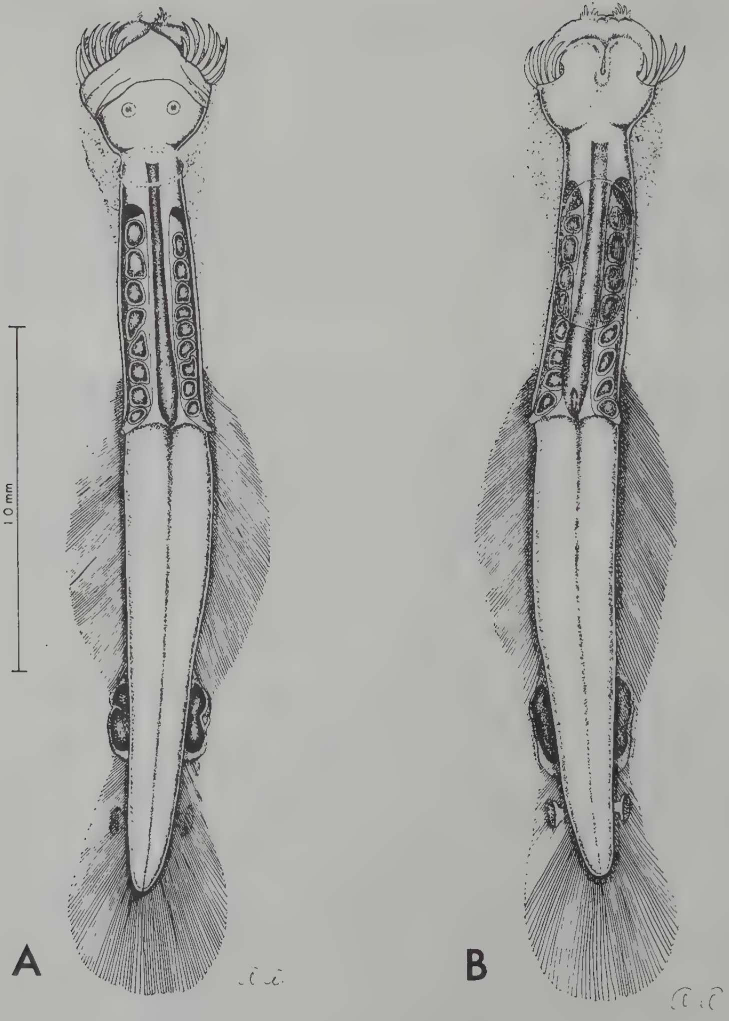

Fig. 1. *Spadella gaetanoi.* A, Dorsal view; B, Ventral view.

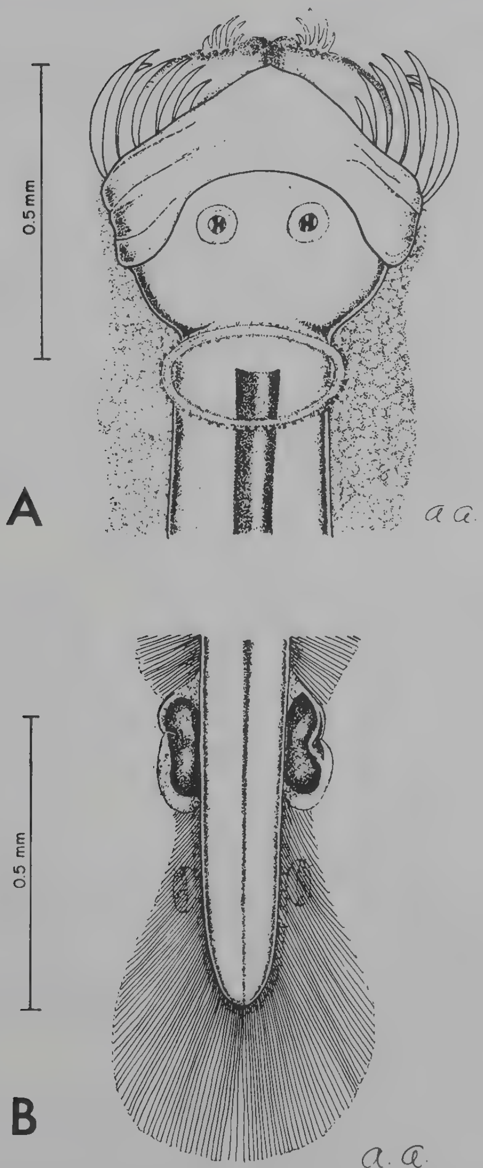

Fig. 2. *Spadella gaetanoi.* A, Dorsal view of head, with detail of hooks, teeth, eyes, corona ciliata, neck, collarette, and anterior part of intestine; B, Dorsal view of posterior part of tail segment, with detail of seminal vesicles and tail fin.

progressing along the tail segment to the tail fin. It is widest at the neck region. Intestinal diverticula absent. The ventral ganglion is large, thick, occupying totally the width and almost half the length of the trunk. It is located at midlength of the trunk, closer to the neck than to the posterior septum.

There is a pair of lateral fins, which are long, narrow, broadest at midlength. They extend from the posterior part of the trunk, from a level anterior to the opening of the oviducts, to the seminal vesicles. They are completely rayed. The caudal fin is long, rounded along the tip of the tail, with a shape as in *Krohnitta pacifica* (Aida) and *K. mutabbii* Alvariño. It is continuous with the lateral fins, by a membranous rayless band which covers the ventral part of the seminal vesicles.

Adhesive digital organs are absent. However, on the ventral side, midway from tip of tail to seminal vesicles, there is on each side a cup-like structure which could have an adhesive function (Fig. 1A, B; Fig. 2B).

The ovaries extend to the neck region, reaching the level of the posterior end of the corona ciliata. The ova are large, in one row, and less than 10 per ovary. The seminal vesicles touch the posterior end of the lateral fins and the tail fin. They are small, reniform. They open at the dorsal side by a latero-dorsal slit at the anterior half of the vesicle. This opening is notch shaped. The ventral extension of the lateral and caudal fins, which cover the ventral part of the seminal vesicles, may function as a soft protecting membranous shield, preventing damage to the vesicles when the animal crawls, and also acting as a device to ensure copulation. During copulation the fins may press against the vesicle to force the release of the gametes, ensuring their entrance to the oviducts (Fig. 2B).

The sensory spots appear distributed at the edges of the ventral and dorsal sides. These structures disappear in part or totally, due to the effect of preservative substances used. Groups of reddish spots observed in other species of *Spadella* were not present in the specimens of *S. gaetanoi*. The animals were fixed in formaldehyde and later transferred to alcohol, which may have destroyed some of the sensory tufts. However, Bieri's specimens of *S. bradshawi* had been maintained in a weak solution of formaldehyde for nearly 20 years, and after that time the orange spots and sensorial papillae could be clearly detected on the animals. The specimens of *S. gaetanoi* had been in preservation only for a few weeks, and the color spots were not evident on the animals.

Remarks.—Spadella gaetanoi differs from *S. cephaloptera* and *S. angulata* in every anatomical characteristic, especially in the absence of the intestinal diverticula, which are present in the two latter species (Table 1). *Spadella gaetanoi* and *S. bradshawi* do not have intestinal diverticula. They differ conspicuously in other anatomical features, including body size, dimensions of ventral ganglion in relation to the length of the trunk, shape of the seminal vesicles and their position in relation to the lateral and

Table 1. Differential characteristics of species of *Spadella* with no digital adhesive organs.

Charact.	S. *cephaloptera* Bush, 1851	S. *angulata* Tokioka, 1951	S. *bradshawi* Bieri, 1974	S. *gaetanoi*, n. sp.
Body length, mm	2–10, firm, broad, wider at posterior septum. Yellow-brownish.	2.5–4–18, including tail fin. Slender, broadest at posterior septum	5.5 to 6.5	2.00 to 3.00
Head	Medium size, neck distinct	Faint orange spots on head		Large, twice as broad as neck.
% tail segment	20–38	51.2–57.9 including tail fin	53–54	53–55
Lateral fins	One pair, long, narrow, from posterior septum to seminal vesicles. Broadest at mid-length	One pair, from posterior part trunk to anterior end seminal vesicles. Broadest at mid-length. No rayless zone. Separated from tail fin	One pair, from level anterior to transverse septum to near seminal vesicles, but not reaching them. No rayless zone.	One pair, from posterior part of trunk to seminal vesicles, joining tail fin over ventral side of seminal vesicles. No rayless zone.
Caudal fin	Long, spatulate starts as posterior end of seminal vesicles	Spatulate	Square spatulate	Roundish-spatulate joining lateral fins at ventral side
Eyes	Pigmented region crescent shape	Pigmented region roundish		Round, prominent. Pigmented region in X shape.
Hooks	7–11, slender, slightly saginated, points sharp, curved	8–10	7–12	8–9 or 10, slender, strongly curved.

Table 1. Continued.

Charact.	*S. cephaloptera* Bush, 1851	*S. angulata* Tokioka, 1951	*S. bradshawi* Bieri, 1974	*S. gaetanoi*, n. sp.
Anterior teeth	2–5, long, thin, innermost longer	2–4	3–5	4–5, long, thin, strongly curved, mid ones on each side are longest.
Posterior teeth	0–4, short, thick	None	None	None, or 4–5, thin, small.
Corona ciliata	Elliptical, rectangular, crescent shape, slightly waved at posterior part, longest axis transverse	Transversely elongated oval, protruding undulation at anterior part.	Oval, massive	Perfect ellipse, extending slightly over collarette
Ventral ganglion		Large, ⅓ of length of trunk	Covers middle ⅓ of trunk	Large, at midlength of trunk, closer to neck than to posterior septum. About half of trunk length
Sensory spots		Evenly spaced, 5 on midline of dorsal side tail segment	4 on midline of dorsal side of tail segment, 2 anterior more spaced than 2 posterior	Along edges of ventral and dorsal sides
Ovaries	Reach neck or anterior end of ventral ganglion. Ova large, close together.	Reach posterior end ventral ganglion. Ova roundish, of regular size.	Reach neck	Reach neck. Ova large, in one row.

Table 1. Continued.

Charact.	*S. cephaloptera* Bush, 1851	*S. angulata* Tokioka, 1951	*S. bradshawi* Bieri, 1974	*S. gaetanoi,* n. sp.
Seminal vesicles	Small, spherical or reniform, touching lateral and tail fins.	Elongated ellipse, breaking at lateral anterior half.	Do not touch tail fin or lateral fins. U shape tube projects to anterior lateral side.	Reniform, breaking by slit of flute point shape, at latero-dorsal side of anterior half.
Intestinal diverticula	Present	Short, distinct.	Absent	Absent.
Adhesive digital organs	None. Adhesive cylindrical cell groups and small glandular lobes on ventral side, mainly on caudal septum.	None	None	None. Adhesive cylindrical disks at ventral side of tail at mid-distance from tip of tail to seminal vesicles.
Collarette	Wide at neck, diminishing in thickness towards tail segment.	Well developed at neck, diminishing thickness towards seminal vesicles.	From head to trunk and tail fin.	Head to tail fin. Thickest at neck region.

tail fins. In S. *gaetanoi* the seminal vesicles touch both lateral fins and tail fin (with a prolongation of those fins covering the ventral side of the seminal vesicles), whereas in S. *bradshawi* the seminal vesicles are separated from both lateral fins and tail fin (Table 1).

Food of Spadella gaetanoi.—The specimens analyzed had been feeding on Copepoda and invertebrate larvae, as those items appeared in the digestive tract in various stages of digestion.

Distribution.—The specimens studied were collected at night at the Kure Atoll (Hawaii) on the western side of the atoll inside the lagoon, on sandy rubble substrata at about 6 m depth. The collections were obtained with an emergence trap attached to the bottom during a survey program by NMFS Honolulu Laboratory on benthic marine communities. With this program Dr. Edmund Hobson and James R. Chess are comparing various marine communities of the leeward islands and the main Hawaiian Islands. Collections were also obtained from Midway Atoll, but S. *gaetanoi* was not found there.

Etymology.—Named after the navigator Juan Gaetano, discoverer of the Hawaiian Islands in 1555. The Hawiian Islands were first named Isles of Volcanoes. They appear in the world map by Juan Martinez (1587), and the map of the Pacific Ocean by Juan Riero Oliva (1591). Cook in his diary and memoirs explains that he was not the first European to visit these islands, and that he knew of the information regarding the discovery of the islands.

Acknowledgments

I would like to express my appreciation to James R. Chess, from NOAA, NMFS Laboratory at Tiburon, California, for his kindness in sending me the material of *Spadella* for identification.

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Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, California 92037.

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Guinea Current upwelling

The historical record of maritime observations are summarised here to indicate the dominant seasonal variations in upwelling, and in certain associated processes, within the Guinea Current region. The region is similar to other eastern ocean boundary upwelling areas in the appearance of cool sea temperatures near the coast, productive coastal fisheries, and a zone of low rainfall on the adjacent coast (Fig. 1). It differs from some of the more studied regions in several important respects. These include the zonal rather than meridional trend of the coast, the influence of a rather narrow intense coastwise current, and an unusual lack of correspondence on the seasonal time scale between sea-temperature features attributable to upwelling, and features in the overlying wind stress field[1]. There seems to be a link between interyear variations in upwelling intensity and corresponding variations in both coastal rainfall and local fishery success.

To construct the sea-temperature distribution shown in Fig. 1, maritime reports for the period 1850–1970 were obtained from the U.S. National Climatic Center's file of marine surface observations (TDF–11), checked for gross errors, and summarised by month and by 1° 'square' areas. Mean values were contoured by hand, taking into account the abundance of observations and magnitude of standard deviations. Data abundance was greatest near the coast and to the west of Cape Palmas. The effect of warm advection in the eastward-flowing Guinea Current is apparent in the shape of the 26 °C isotherm and in the offshore temperature maximum which separates the cool temperatures along the coast east of Cape Palmas, attributable to coastal upwelling, from cool temperatures near the equator which are probably related to equatorial upwelling.

The seasonal distribution of sea-surface temperature within a line of 1° square areas stretching southward from the coast near Cape Three Points (Fig. 2) features an offshore maximum every month, suggesting continuation of some degree of coastal upwelling throughout the year. The offshore gradients are most intense from June through October; coolest coastal temperatures are reached during August and September. A secondary coastal minimum appears during January, resulting in a two-peaked annual temperature cycle.

A similar display of the seasonal cycle of sea-surface temperature (Fig. 3), this time within a line of 1° square areas arranged along the coastal boundary, reveals continuity of the summer minimum along the entire north coast of the Gulf of Guinea. In Fig. 3, west is towards the top (see Fig. 3*d*); thus the direction of flow of the Guinea Current is from the top towards the bottom of the diagram. The temperature decreases in the direction of flow to an absolute minimum east of Cape Three Points. Although the contour interval in Fig. 3 is too coarse to show it, much of the temperature decrease occurs in two abrupt steps upon passing each of the two major capes, Cape Palmas and Cape Three Points. Particularly sharp temperature gradients have been reported off Cape Palmas[2]. The coolest region, defined by the 24°C isotherm, appears in Fig. 3 to be split into two lobes by slightly higher temperatures from 0–1°W longitude; this is an artefact due to that particular 1° square being displaced slightly offshore relative to the squares to either side. Eastward of this late summer minimum feature, sea-surface temperature increases towards a region increasingly affected by outflow from the Niger River Delta and other sources. A cold temperature feature is apparent during winter in the extreme western portion of the region. The sharp gradient near 15°W longitude indicates the southern limit of the tropical front which oscillates seasonally along the west African coast between 10°N and 20°N latitudes, apparently responding to seasonal variations in wind-induced upwelling and associated along shore advection[3]. Extending eastwards from the front is a winter temperature minimum which retains its identity along the Guinea Coast well into the Bight of Biafra (~7°E longitude) where it is evident as a slight reversal during January. The two seasonal temperature minima are separated by periods of relatively warm sea-surface temperatures, with the major maximum occurring during spring.

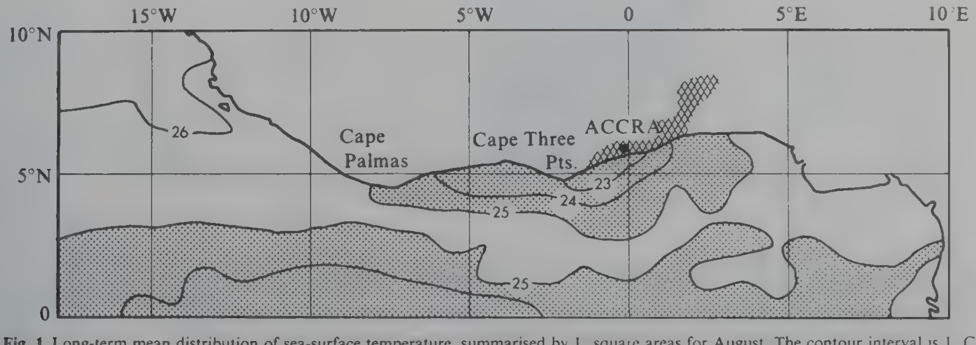


Fig. 1 Long-term mean distribution of sea-surface temperature, summarised by 1° square areas for August. The contour interval is 1 °C; temperatures less than 25 °C are shaded. The crosshatched area on the coast in the vicinity of Accra indicates an area of less than 40 inches annual rainfall, and defines the approximate extent of the Accra dry belt[16].

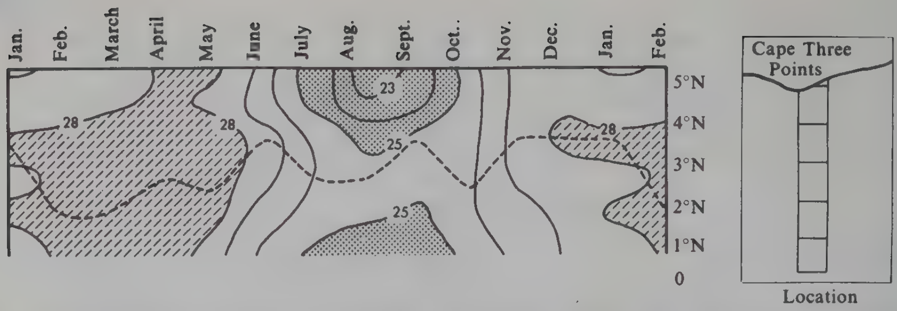
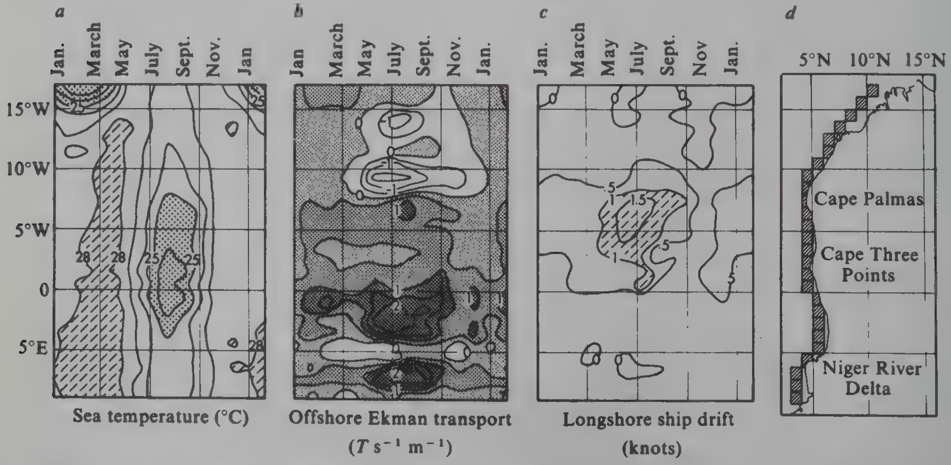


Fig. 2 Long-term composite annual cycle of sea-surface temperature within the line of 1° squares normal to the coast near Cape Three Points shown to the right. The contour interval is 1 °C; temperatures less than 25 °C are shaded, and those greater than 28 °C are indicated by broken diagonal hatching. The location of the maximum mean temperature within the line of squares for each long-term monthly sample is indicated by the dashed line.

Being near the equator, the Guinea Current region experiences two periods of vertical sun per year, one shortly before the vernal equinox and the other shortly after the autumnal equinox. Unlike the situation in more temperate latitudes, both solstices are periods of low sun. Thus, the double peaked seasonal cycle of sea temperature matches qualitatively the cycle of solar height. But compilations of mid-ocean sea-surface temperatures[4], at similar latitudes where the cycle of solar height is identical, indicate no such strong correspondence. Thus, it is difficult to ascribe the observed features directly to such large scale effects as passages of the Sun. Rather, they would seem to be almost entirely controlled by processes local to the Guinea Current region.

In the classical model for coastal upwelling[5], water set in motion by the stress of the wind is deflected offshore by the rotation of the Earth. When this occurs along an extensive stretch of coast such that the water transported off the coast cannot readily be replaced by convergence of horizontal alongshore flow, replacement can occur by upwelling of deeper water.

Previous comparisons of offshore Ekman transport distributions with corresponding temperature distributions in the California Current[6], and Canary Current[3] regions on a similar 1° scale have yielded general conformities in major features, indicating seasonal variation in the local wind as the principal factor controlling seasonality in the coastal upwelling process. Accordingly, wind reports from the Guinea Current region were assembled from the same source as the temperature reports. These were converted to measures of sea-surface stress by squaring each reported wind speed and multiplying by the density of air (assumed constant, 0.00122 g cm^{-3}) and a constant drag coefficient (0.0013). The derived stress 'reports' were then averaged by components to yield a resultant mean stress for each long term composite month and 1° square area. This was con-



Sea temperature (°C)

Offshore Ekman transport ($T\,s^{-1}\,m^{-1}$)

Longshore ship drift (knots)

Fig. 3 Long-term composite monthly variations within the 1° square areas arranged along the coast, shown in (*d*). *a*, Sea-surface temperature. The contour interval is 1 °C; temperatures less than 25 °C are shaded and those greater than 28 °C are indicated by broken diagonal hatching. *b*, Offshore-directed component of Ekman transport. The contour interval is 0.5 tonnes S^{-1} transported across each 1 m width. Positive values, indicating seaward transport, are shaded; darker shading indicates more intense seaward transport. *c*, Alongshore component of ship drift. The positive direction is such that the coast is on the left when facing downstream. The contour interval is 0.5 knots; speeds greater than one knot are indicated by broken diagonal hatching.

verted to Ekman transport, directed 90° to the right of the stress vector, by dividing by the Coriolis parameter computed at the mid latitude of the 1° square. Where the centre of the square is less than 5° from the equator the value of the Coriolis parameter at 5°N latitude was used. Offshore components were resolved along characteristic offshore normal directions, based on the nearshore bathymetry within each individual square.

The seasonal pattern of offshore-directed Ekman transport (Fig. 3) reveals certain features which correspond to features in the temperature pattern. Transport tends to be offshore throughout the year, except during certain months off Liberia and Sierra Leone (8–14°W) and near the west-facing portion of the Niger River Delta shoreline (4–6°E). A winter maximum of offshore transport occurs in March at the northwestern end of the area (top of the diagram), and retains continuity toward the east, shifting to February off Cape Palmas and Cape Three Points. This winter maximum generally corresponds to the winter temperature minimum described above. During the summer there is a relative maximum of offshore Ekman transport on the east side of Cape Palmas and another increase to the east of Cape Three Points; these correspond to the major decreases in sea temperature near these capes.

Maximum values of offshore transport occur to the east, however, that is downstream in relation to Guinea Current flow, of the location of summer minimum temperatures. The offshore transport maximum off Dahomey (2–4°E) is in the area of most rapid down-stream warming. Likewise, a second offshore transport maximum in the Bight of Biafra (6–9°) is not strongly reflected in the sea-temperature distribution, although both cases may involve some masking of the effects of upwelling by low salinity surface water. Certainly, there is nothing in the local Ekman transport distribution to account for the continuity of the temperature minimum to the west, that is, upstream, of Cape Palmas.

Since this region is very near the equator, the diminished Coriolis term in the dynamical equations may lead to a different balance of forces from that assumed in the Ekman transport relationship. In such a case the transport could be at a lesser angle than 90° to the direction of wind stress. Such an effect, however, cannot explain the non-correspondence of the distributions in Fig. 3. Summaries of wind observations produced as part of this study show a very significant component of the mean wind to be directed onshore at all seasons. Any larger portion of the transport being directed with the wind would, therefore, only imply a further reduction in local wind forcing of upwelling at the coast.

Figure 3*c* summarises reports of drift attributed to ocean currents compiled from ship's logbooks by the U.S. Naval Oceanographic Office. Although the number of available reports is very small, being of the order of 20 per month-square in the area from Cape Palmas to Cape Three Points, a coherent picture of the seasonal cycle of flow in the Guinea Current is apparent. Off Cape Palmas the current near the coast intensifies dramatically, diminishes slightly toward Cape Three Points, and drops off rapidly past Cape Three Points. Mean velocities near Cape Palmas vary from nearly 2 knots in July to less than half a knot in November. The current maximum is thus somewhat upstream of and slightly preceding the summer temperature minimum, actually coinciding in time to the period of most rapid temporal decrease of temperature and in space to the zone of most rapid spatial decrease. Horizontal advection in the current, of course, opposes the temperature decrease. Various mechanisms leading to vertical advection in an intensified current[7-10] could perhaps contribute to the observed cooling. But, the lag of at least a month between the maximum current speed in July and the minimum sea-surface temperatures in August–September (Fig. 3) is difficult to reconcile with any predominant effect of such processes; for example, at the indicated average current velocities, water upwelled near Cape Palmas during the July current maximum would be carried past Cape Three Points in less than 10 days.

Recent theoretical developments have indicated the ability of upwelling-produced displacements of the internal density structure to propagate in the form of coastal trapped waves, and thus to affect the temperature and current velocity fields at other locations along the coast[11,12]. In the configuration of the Guinea Current region, the direction of propagation would be to the west. The degree of westward displacement of features in the sea temperature and drift patterns, compared to features in the Ekman transport field (Fig. 3), is consistent with computations from theory

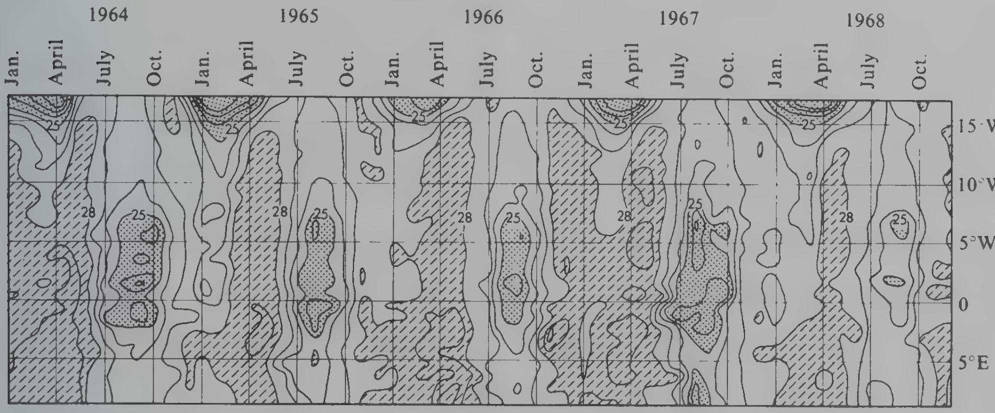


Fig. 4 Monthly temperature variation within the square areas shown in Fig. 3, during the years 1964 through 1968. The contour interval is 1 °C; temperatures less than 25 °C are shaded and those greater than 28 C are indicated by broken diagonal hatching.

Table 1 Comparison of intensity of summer-fall upwelling with July–October rainfall at three reporting stations in Ghana and with catch of the Ghanaian herring fishery for the years 1964 through 1968

		1964	1965	1966	1967	1968
Upwelling		High (late)	Intermediate	Intermediate	High	Low
Month		J A S O*	J A S O	J A S O	J A S O	J A S O
Rainfall (quintiles)	Accra	3 1 0 0	5 5 3 2	4 3 1 3	1 2 5 1	6 6 6 5
	Takoradi	2 4 1 0	4 4 5 1	5 4 2 2	2 2 3 1	6 6 6 5
	Kumasi	3 4 1 2	4 5 3 5	6 5 1 2	2 1 2 1	6 6 6 1
Summation		21	46	38	23	65
Herring catch (Ghana)		34.2	7.8	13.3	43.2	12.2

Upwelling intensity is estimated from sea-temperature distributions (Fig. 4). Rainfall is given in quintiles of the frequency group within which the recorded precipitation falls relative to a group of reference years[17]. 0 indicates monthly precipitation to have been lower, and a '6' indicates it to have been higher, than in any corresponding month in the reference series. In the line labelled summation the quintile values for the four months and the three stations are added together to give a seasonal index. The herring catch is in 10^3 tonnes.

*J, July; A, August; S. September; O, October.

(A. J. Clarke, personal communication). Thus it seems that such processes may be exerting particularly strong control on the pattern of seasonal upwelling in the Guinea Current.

In the surface marine observation file (TDF–11) there is an abrupt increase in the density of reports in the Guinea Current region beginning with 1964. In the particular version of the file that was used in this study, however, the frequency begins to drop off rapidly after 1968. For these five years of maximum data density a time series of sea-surface temperature (Fig. 4) was constructed on the same basis as the long-term composite annual cycle (Fig. 3). Because of the higher short-term variance of the wind, the data density was not sufficient to derive a meaningful similar series of wind or Ekman transport variations.

If one examines the summer upwelling feature (10°W–5°E longitude) in Fig. 4, it is possible to class the summers of 1964 and 1967 as having been cold (strong upwelling), 1968 as having been warm (weak upwelling), and 1965 and 1966 as having been intermediate (Table 1). In addition the strong upwelling in 1964 seems to have occurred relatively late, the coolest monthly mean temperatures appearing in September rather than in August as is the case in long-term composite cycle (Fig. 3). In partial corroboration of this classification, dissolved oxygen data collected off Ivory Coast (~4°W) during the period 1966–70[13] show low oxygen values characteristic of deeper layers unmistakably nearer the surface during the summer upwelling season of 1967 than in the other years of that particular series.

With these upwelling estimates, it is possible to look for apparent effects of upwelling variations on coastal rainfall. One mechanism which may contribute to the intense coastal aridity, which is a general characteristic of upwelling regions, is the stabilisation of the shoreward airflow by the cool upwelled surface waters, thereby inhibiting vertical development of storm clouds[14]. The Accra dry belt (Fig. 1), which has the appearance of a coastal enclave of semi-arid savanna surrounded by tropical rainforest, has been termed 'the most remarkable climatic anomaly of the Guinea coastlands'[15]. One of the unusual features cited is an anomalous dearth of rainfall during the late summer. Prevailing winds are from the south-west[16]; Figure 1 shows the Accra dry belt to be oriented directly downwind of the coldest sea-surface temperatures.

Table 1 classifies the rainfall recorded at three locations in Ghana[17]. Takoradi is located on the coast, just east of Cape Three Points. Kumasi is about 100 miles inland, between Takoradi and Accra. The correlation of the rainfall record with the upwelling estimates is convincingly strong. During the years of strong upwelling, 1964 and 1967, the July–October rainfall was anomalously low; in fact 'late' upwelling estimated for 1964 corresponds to 'late' rainfall deficits in September and October. During the weak upwelling year, 1968, monthly mean rainfall actually exceeded the highest class intervals established from historical data at all three locations during the months of July, August, and September.

Also listed in Table 1 are the landings of herring (*Sardinela aurita*) in Ghana during these same five years[18]. This was Ghana's most important fishery during this period, largely operating from canoes very near shore during the summer-fall upwelling period[19]. Evidently periods of extremely good fishing were associated with strong upwelling, as are periods of subnormal coastal rainfall. During these years a sharply increased trend in fishing effort occurred, due to technology and so on. If this is taken into account in interpreting the landing figures, a relationship is even more apparent.

ANDREW BAKUN

Pacific Environmental Group,
Southwest Fisheries Center,
National Marine Fisheries Service, NOAA, Monterey,
California 93940

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CLIMATOLOGY OF UPWELLING RELATED PROCESSES OFF BAJA CALIFORNIA

ANDREW BAKUN AND CRAIG S. NELSON

Pacific Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service, NOAA
Monterey, California 93940

ABSTRACT

Marine surface data are used to describe large scale features of upwelling and certain related processes off the west coast of Baja California. The offshore-directed component of sea surface Ekman transport, computed from the wind stress distribution, is considered an index of coastal upwelling intensity. Upwelling appears to be strongest south of 30°N latitude, from March to June. Departures from randomness in the offshore Ekman transport signals include the annual and diurnal periodicities, an energetic irregular rhythm in the "event" frequency range (several day to several week periods), and two types of persistence. A short-term persistence appears to be related to the duration of synoptic scale atmospheric disturbances, while a much longer-term persistence may be related to a feedback mechanism between the upwelling and the overlying wind stress field.

The longshore current field is highly correlated seasonally with the upwelling cycle. Strong equatorward surface flow is indicated during the spring upwelling maximum; during the fall there is generally a poleward component of flow. Wind stress curl distributions indicate a tendency for the surface wind drift to be convergent (negative curl) in the offshore region. From Punta Baja to Punta Eugenia the convergent area extends to the coast. Areas of divergent surface drift (positive curl) extend several hundred kilometers off the coast north of Punta Baja and south of Punta Eugenia. From a "Sverdrup transport" point of view, this pattern is consistent with evidence of separate cyclonic gyral circulations north of Punta Baja and south of Punta Eugenia.

INTRODUCTION

Coastal upwelling is a highly fluctuating process which can have important effects on fishery resources. The role of upwelling in bringing nutrients into the surface layers where they are available for organic production is widely recognized. A related process that may enhance production is the dispersion of grazing organisms by the diverging surface waters, thereby reducing grazing pressure on the phytoplankton stock. In addition to these effects at the very base of the food web, upwelling can alter the temperature distribution, field of motion, stratification, and other characteristics of the physical environment, affecting marine organisms at various levels of their life processes.

At the Pacific Environmental Group we are developing descriptions of upwelling phenomena to aid fishery researchers in accounting for such effects. To be most useful these descriptions should have continuity over the broad space scales and long time scales involved in fishery work. In addition it is desirable that they be continually updated and hindcast over past periods for which knowledge of a fishery is available. Our approach, consequently, has been to avoid basing our work on dedicated observational programs but rather to try to construct a useful descriptive system from observatons routinely reported by ships at sea, weather stations, etc.

Our collocation with the U.S. Navy's Fleet Numerical Weather Central (FNWC) in Monterey, California, provides access to a broad data base including archived historical data, analyzed meteorological products, and real time reports. Several data sources have proven most fruitful. The National Climatic Center's file of marine surface observations has been useful in defining the climatological seasonal cycles. This file contains over 38 million individual ship reports, dating back into the nineteenth century. Similar real-time ship reports continue to be delivered via the international data networks. To describe variations from normal seasonal conditions we have used the analyzed products, notably the surface atmospheric pressure analysis, produced by FNWC. Finally, the U.S. Naval Oceanographic Office ship drift file, which is a compilation from ships' log books of differences between dead reckoning position and accurately detemined position, has been useful as an indication of the seasonal variability of the ocean surface flow field.

Our major focus is the upwelling region off western North America. However, since the data sources are global the methods developed should be applicable to other regions, depending on the density of available data. At this stage much of our work is qualitative. Our goal is to model quantitatively many of the processes which would be useful environmental inputs to fishery management systems for upwelling regions, and to define and develop practical indicator systems to make these inputs operational.

THE SEASONAL CYCLES

To define seasonal variations, long-term composite monthly distributions of various properties were assembled from ship reports contained in the National Climatic Center's file of marine surface observations (TDF-11). After preliminary gross error checks, similar to those described by Bakun, McLain, and Mayo (1974), climatological scalar properties were compiled by computing the arithmetic means of all available reports within a specified 1-degree square area and long-term (1850–1970) month. Similarly, resultant mean vector quantities have been computed as the arithmetic means by north and east components for all reports in the area. A mean value for any month and square is therefore formed from a data set that is independent of all other months and squares. No attempt has been made to smooth the fields, either by removing data which do not appear to fit the distributions or by applying objective smoothing procedures. The mean values were contoured by machine, and "bulls eyes" in the contours, even where they possibly reflect erroneous data, were left in the figures as indications of the general degree of consistency of the composite fields.

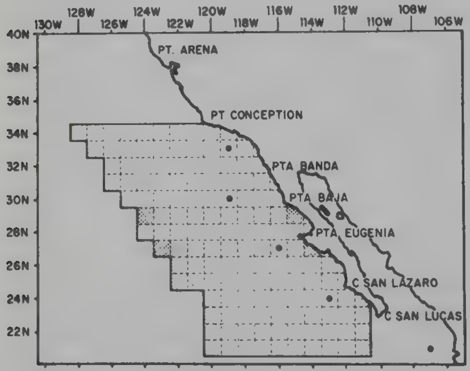


FIGURE 1. Chart of the Baja California region. The grid of 1 degree squares is used for summaries of ship observations. Shading indicates nearshore and offshore lines of selected squares parallel to the coast and lines extending westward from the coast south of Punta Baja and Punta Eugenia used for displays of time-space sections. Large dots indicate 3 degree grid intersections used to compute time series properties.

Approximately 400,000 individual reports are available for the area defined by the grid off southern California and Baja California (Figure 1). The number of reports per 1-degree square per month varies from less than five (in May in the southwest section of the grid), to 3500 (in May off Los Angeles). The spatial distribution of observations is biased in that "ship of opportunity" reports are generally confined to coastwise shipping lanes. The highest density of reports is found within 3 degrees of the coast and north of 30°N latitude. Significant temporal bias may exist, since approximately 50% of the total available observations have been taken since 1945. Nevertheless, the coherence of the resulting vector and scalar fields indicates that our composite distributions can be used to describe the dominant seasonal cycles in upwelling related processes. Moreover, comparisons between our monthly sea surface temperature fields and those of Robinson and Bauer (1971), for example, show good correlation.

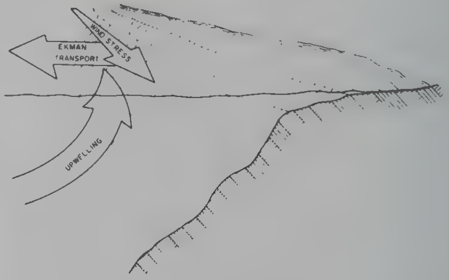


FIGURE 2. A conceptual diagram of the coastal upwelling process. The coast of the continent is represented in cutaway view with the ocean to the left of the figure. Offshore transport in the surface Ekman layer of the ocean due to stress of the wind is replaced by upwelling from depth.

In a simplified view of the coastal upwelling process, equatorward wind stress parallel to the coast induces flow in the surface layers of the ocean which is deflected offshore by the earth's rotation (Figure 2). When this occurs over a wide expanse of coast where longshore horizontal surface flow cannot compensate for that driven offshore, the balance is maintained by upwelling of deeper water. Wooster and Reid (1963) approximated the wind-driven offshore flow as Ekman transport and showed that this "index of upwelling" explained in general the observed features of coastal upwelling in broad diffuse eastern boundary currents such as exists off Baja California.

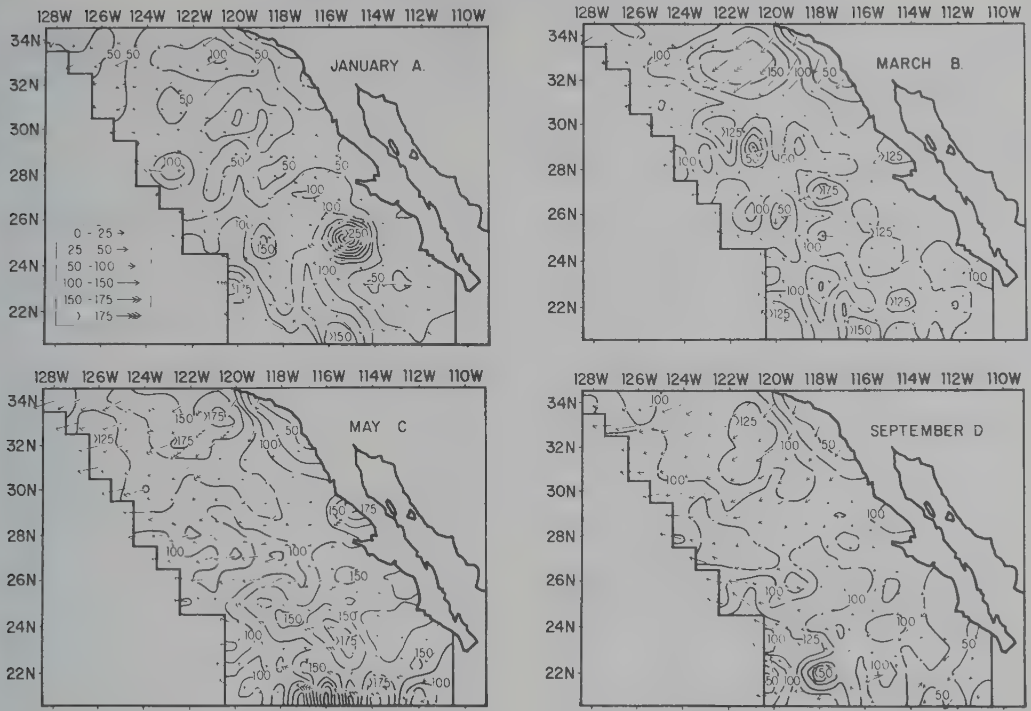


FIGURE 3. Sea surface wind stress. Monthly composite fields of resultant vectors were summarized by 1 degree squares from historical ship observations for A. JANUARY, B. MARCH, C. MAY, and D. SEPTEMBER. Units are dynes/cm². Magnitudes are contoured at intervals of 0.5 dynes/cm². Vector symbols are scaled according to the key.

Wind Stress

In producing the long term composite monthly sea surface wind-stress distributions (Figure 3), the stress was calculated from each wind velocity report according to

$$\tau = \rho_a \, C_D \, |\vec{v}| \, \vec{v} \qquad (1)$$

where:

$\vec{\tau}$ denotes the stress vector

ρ_a is the density of air which was considered to have a constant value of 0.00122 g/cm³

$|\vec{v}|$ is the observed wind speed

$\vec{v}$ is the observed wind velocity vector

C_D is an empirical drag coefficient.

A constant drag coefficient of 0.0016 (Denman and Miyake, 1973) was employed.

The fields show the tendency for an equatorward component of stress to parallel the coast of Baja California, which implies conditions favorable for upwelling throughout the year. Most of the seasonal variability appears in magnitude rather than in direction. A wind stress maximum appears south of Point Conception in March. During May (Figure 3C), stress exceeds 1.0 dyne/cm² within the region north of 30°N latitude, while values for most of the offshore region to the south lie between 0.5 and 1.0 dyne/cm². The maximum immediately north of Punta Eugenia is a consistent feature during the spring. The mean distributions for January and September (Figures 3A and 3D) indicate relaxed conditions. Typical values of surface stress are less than 0.5 dyne/cm². A region of minimum wind stress is indicated along the coast from Point Conception to Punta Banda. This feature corresponds in location to the cyclonic eddy which dominates the ocean surface circulation in the Southern California Bight (Reid, Roden, and Wyllie, 1958).

Surface Wind Transport

Our estimates of the transport in the surface layer of the ocean due to the stress of the wind are based on Ekman's (1905) theory which leads to the following equation for the total integrated mass transport of pure drift currents:

$$\vec{V}_E = \frac{1}{f}\vec{\tau} \times \vec{k} \qquad (2)$$

where:

$\vec{V}_E$ is the total mass transport resulting from an applied local wind stress

f is the Coriolis parameter

$\vec{k}$ is a unit vector directed vertically upward

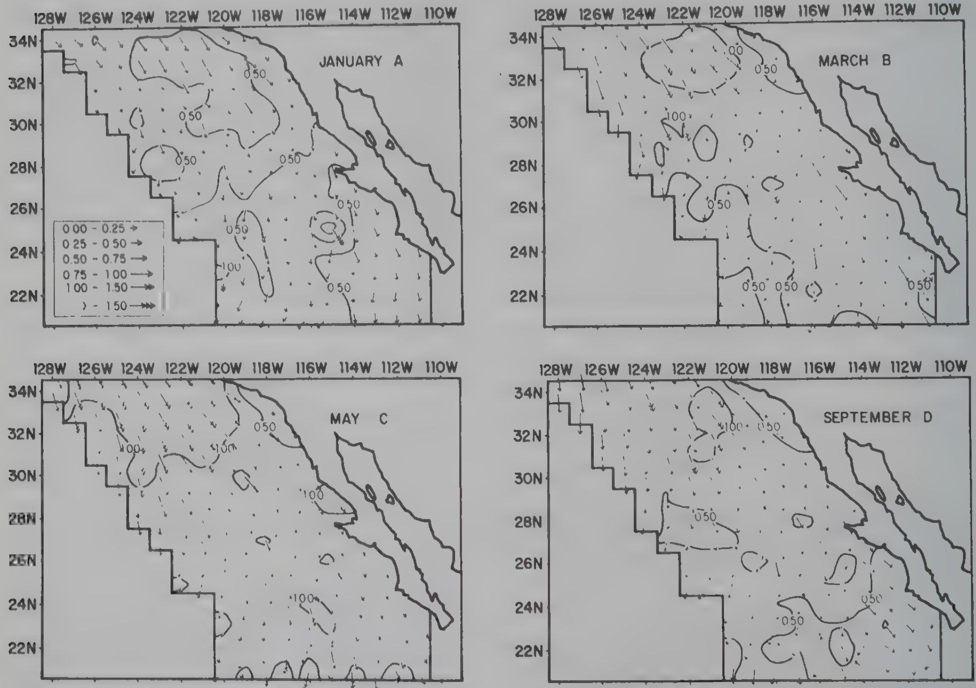


FIGURE 4. Surface Ekman transport. Monthly composite fields of resultant vectors were summarized by 1 degree squares from historical ship observations for A. JANUARY, B. MARCH, C. MAY, and D. SEPTEMBER. Units are metric tons per second per 100 meters coastline. Magnitudes are contoured at intervals of 25 units. Vectors symbols are scaled according to the key.

The relationship implies that the integrated transport is directed 90° to the right of the wind stress in the northern hemisphere.

Composite monthly fields of Ekman transport (Figure 4) were calculated by applying equation (2) to the mean distributions of surface wind stress. The mean transport is directed offshore throughout the year. Accordingly, our conceptual model (Figure 2) indicates strong upwelling in regions of coastal divergence in March and May (Figures 4B and 4C). During these months local maxima in the surface transport appear north of 30°N latitude, immediately north of Punta Eugenia, and south of 24°N, where the decrease in the Coriolis parameter leads to corresponding increases in the computed Ekman transport. Offshore gradients in the surface transport may contribute to convergences and divergences, thereby altering the distributions of organisms.

The seasonal cycle of Ekman transport (Figures 5 and 6) within the selected 1-degree squares adjacent to the coast (Figure 1) indicates the general seasonal pattern of local wind forcing of coastal upwelling. The degree of correspondence in general shape and position of the contours of absolute magnitude in the vector time series (Figure 5) with the contours of magnitude of the offshore component (Figure 6) illustrates the primarily offshore direction of wind driven surface flow off Baja California, implying some degree of upwelling on average throughout the year. Strongest upwelling appears to occur from March to June, and along the coast from 20°N to 30°N.

A maximum is apparent north of Punta Eugenia at 28°N latitude. From September to December, offshore transport weakens, and changes sign in September at 21°N. July and August, and January and February appear to be transition periods.

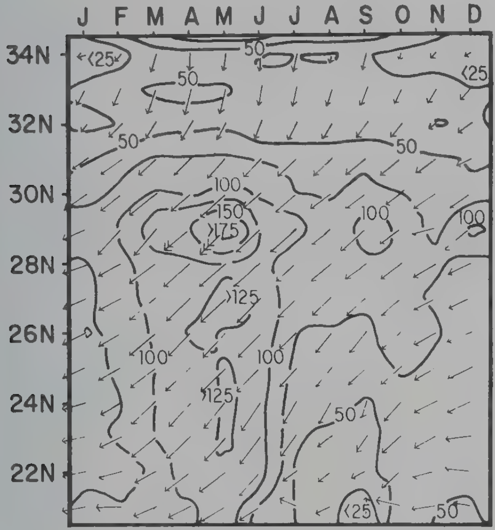


FIGURE 5. Seasonal cycle of Ekman transport near the coast. Resultant vectors were summarized by month for the group of selected 1 degree squares adjacent to the coast shown in Figure 1. Units are metric tons per second per 100 m coastline. Magnitudes are contoured at intervals of 25 units. Vector symbols are scaled according to the key in Figure 4A.

In addition to the surface Ekman wind drift, the ocean surface flow field also contains geostrophic components. Sverdrup, Johnson, and Fleming (1942, page 501) describe a linkage by which the accumulation of denser upwelled water near the coast and the transport away from the coast of lighter surface water leads to a redistribution of mass. The balance between the resulting pressure gradient and the Coriolis force produces a geostrophic current in the equilibrium state. Consequently, on a seasonal basis, one might expect variations in the offshore component of Ekman transport to be well correlated with variations in longshore flow. Indeed, investigators in CUEA have demonstrated this correspondence on shorter time scales (Huyer, et al., 1974).

Surface Currents

The only available direct measurements of ocean surface flow having reasonable spatial and seasonal coverage are reports of drift attributed to ocean currents, compiled from ships' log books. We have made seasonal summaries from the ship drift file of the U.S. Naval Oceanographic Office. These data are much the same as used by Wyrtki (1965). The density of available reports is only about one-tenth that of marine surface observations and is dependent upon the primary coastwise shipping lanes. Significant bias by month and year is apparent; March, May, and November contain approximately two to four times as many observations as any other month, and most of the observations were reported prior to 1940.

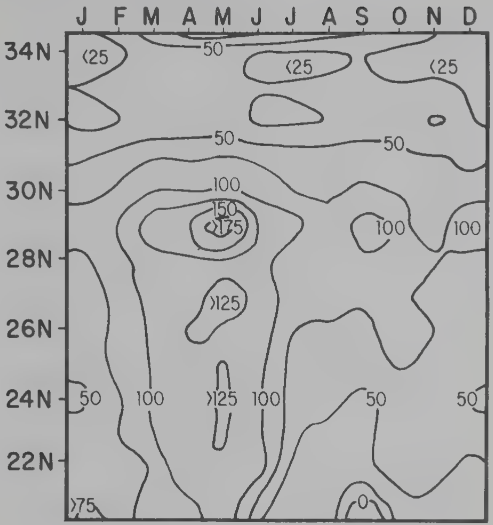


FIGURE 6. Seasonal cycle of offshore Ekman transport. Means of offshore components of Ekman transport were computed by month within the group of selected 1 degree squares near the coast shown in Figure 1. Units are metric tons per second per 100m coastline. Onshore Ekman transport is shaded.

Ship drift distributions are inherently noisy and require a large data base to resolve the underlying patterns. To increase the number of observations per averaged value, we have used summaries by 2-degree squares, by month (Figures 7 and 8), and by quarter (Figure 9). The precise interpretation of these measurements remains open to question since wind effects on reporting vessles are indeterminate. However, Stidd (1974) has indicated a closer correspondence of ship drift to ocean current direction than to wind direction. In addition, mean ship drift vectors are in some cases directed oppositely to mean wind vectors. The Southern California Countercurrent is an example.

A significant correlation between the longshore component of surface current (Figure 8) and the offshore component of Ekman transport (Figure 6) is apparent. Specifically, during the period of maximum offshore transport, equatorward surface flow in the California Current is strongest. Indeed, there is a correspondence between the position of

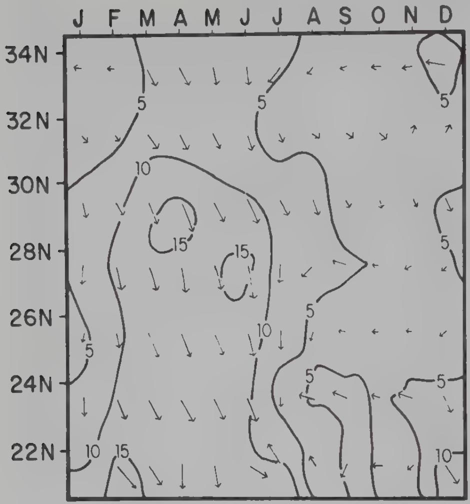


FIGURE 7. Seasonal cycle of ship drift near the coast. Resultant vector were summarized by month from the NAVOCEANO ship drift file, for a group of 2 degree squares along the coast from latitude 20°N to 34°N. Units are cm/sec. Magnitudes are contoured at intervals of 5 cm/sec. Vector symbols are scaled according to the key in Figure 9A.

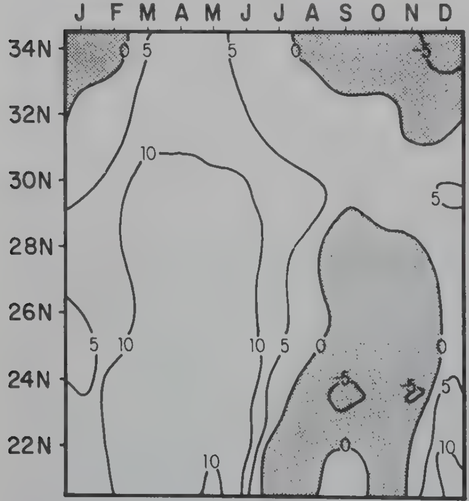


FIGURE 8. Seasonal cycle of longshore ship drift. Means of components parallel to the coast were summarized from the NAVOCEANO ship drift file for a group of 2 degree squares along the coast from latitude 20°N to 34°N. Units are cm/sec. Positive values indicate equatorward drift. Poleward drift is shaded.

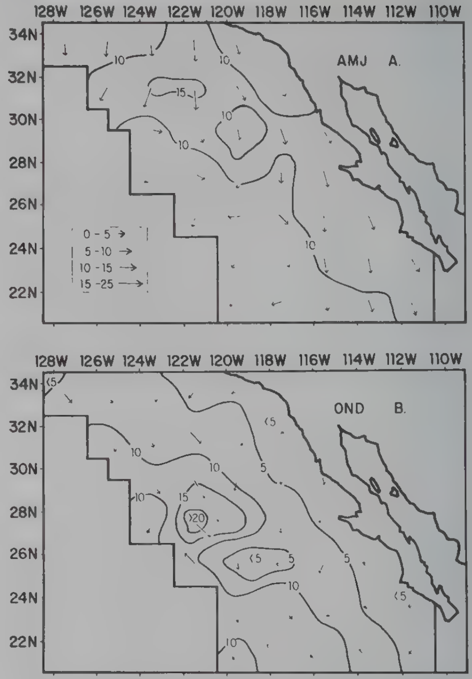


FIGURE 9. Ship drift. Composite field of resultant vectors were summarized by quarter and by 2 degree squares from the NAVOCEANO ship drift file for A. APRIL-MAY-JUNE and B. OCTOBER-NOVEMBER-DECEMBER. Units are cm/sec. Magnitudes are contoured at intervals of 5 cm/sec. Vector symbols are scaled according to the key.

the maximum offshore Ekman transport north of Punta Eugenia (Figure 5) and the position of the strongest longshore surface currents at latitude 29° N in April and May (Figure 7). During the relaxed period of upwelling, from September to December, the surface current changes direction and flows offshore, but has a definite poleward component along the coast. The surface current data indicate cyclonic flow in the Southern California Bight, where offshore Ekman transport is less than 50 metric tons per second per 100 m of coastline throughout the year. These data suggest that the surface countercurrent off Baja California may only form where offshore Ekman transport is weak.

During the spring upwelling season, surface current parallels the coast with only a slight offshore component (Figure 9A) and reaches a maximum strength of about 15cm/sec (Figure 7). During the period of relaxed upwelling, the current changes direction and slows to less than 5 cm/sec (Figure 9B). Flow is primarily offshore, but there is some suggestion of a coastal countercurrent. The lack of coherence in the distributions between 7 and 10 degrees off the coast reflects scarcity of data.

Sea Surface Temperature

Vertical and horizontal advection associated with coastal upwelling alter the patterns of surface isotherms which are approximately zonally distributed off Baja California. The composite surface temperature field for June (Figure 10) shows cold water indicative of upwelling along the coast from Punta Eugenia to Punta Baja. This feature correlates well with the local Ekman transport maximum in the same area. South of latitude 25° N, indications of upwelling in the temperature distribution are slight. In the region off southern California, the warm coastal temperatures may reflect seasonal heating and warm advection in the cyclonic eddy (Reid, Roden, and Wyllie, 1958).

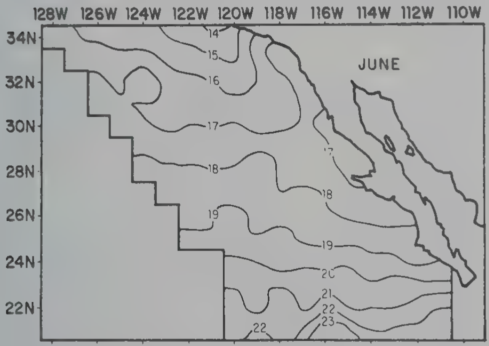


FIGURE 10. Sea surface temperature during June. Mean values of sea surface temperature observations were computed by 1 degree squares for the month of June. Units are degrees Celsius.

The coarse resolution in the 1-degree spatial summaries used in this paper tends to mask fine scale features of the temperature distributions. These particular temperature fields were developed to be compatible in resolution to, and used in conjunction with, our other data fields. More detailed treatments can be found in California Marine Research Committee (1963), Lynn (1967), and Wyllie and Lynn (1971).

The seasonal cycle of the sea surface temperature offshore (Figure 11) shows a normal north-south temperature gradient and a seasonal warming-cooling cycle with a typical range of 2° C to 4° C. Minima occur from February to March and maxima from August to September.

Comparison of the temperature cycle near the coast (Figure 12) with that occurring offshore (Figure 11) shows differences which may be largely

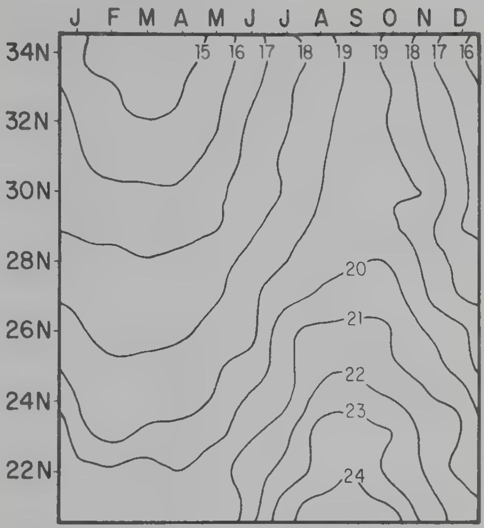


FIGURE 11. Seasonal cycle of sea surface temperature in the offshore region. Mean values of sea surface temperature observations were computed by month for the group of selected 1 degree squares indicated in Figure 1 at the offshore edge of the grid. Units are degrees Celsius.

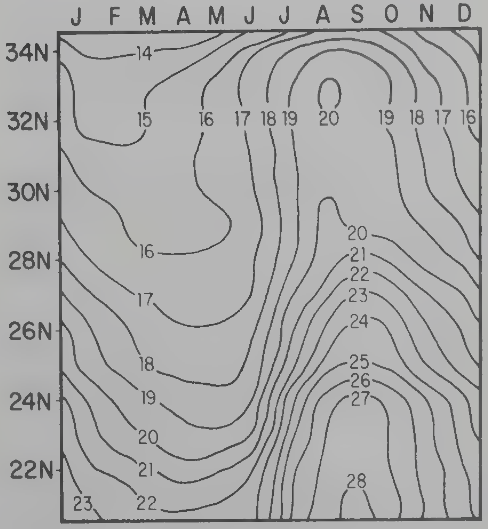


FIGURE 12. Seasonal cycle of sea surface temperature near the coast. Mean values of sea surface temperature observations were computed by month for the group of selected 1 degree squares adjacent to the coast, indicated in Figure 1. Units are degrees Celsius.

attributable to the effect of coastal upwelling, and to differences between horizontal advection in the offshore region and that in the coastal region. There is also the possibility of significant spatial differences in ocean-atmosphere heat exchange. Near the coast the seasonal temperature minimum is delayed relative to that offshore, occurring from March to May in phase with the maximum offshore Ekman transport. A more rapid increase of temperature near the coast during early summer, corresponding to the weakening of the southward surface flow (Figure 7), leads to significantly higher temperatures near the coast during summer than at the same latitude offshore.

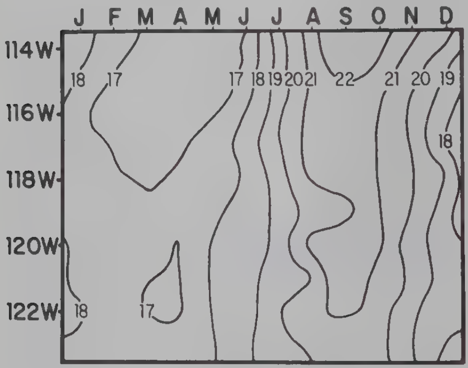


FIGURE 13. Seasonal cycle of sea surface temperature off Punta Eugenia. Mean values of sea surface temperature observations were computed by month for the group of selected 1 degree squares extending westward from the coast south of Punta Eugenia, indicated in Figure 1. Units are degrees Celsius.

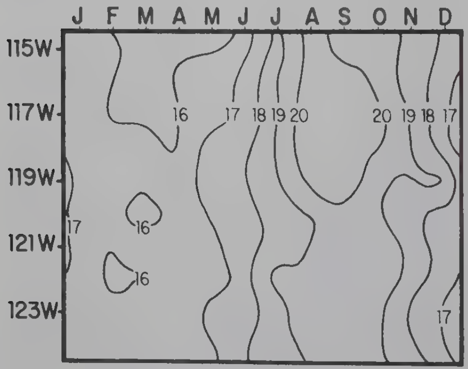


FIGURE 14. Seasonal cycle of sea surface temperature off Punta Baja. Mean values of sea surface temperature observations were computed by month for the group of selected 1 degree squares extending westward from the coast south of Punta Baja, indicated in Figure 1. Units are degrees Celsius.

Time series displays of seasonal sea surface temperatures in lines of squares extending westward from the coast (Figures 13 and 14) show colder water appearing near the coast in March. The gradients extend several hundred kilometers offshore during spring. During early summer, advection and possible spatial variations in ocean-atmosphere heat exchange processes offset the upwelling indicated by a continued, although weakened, offshore Ekman transport (Figure 6), leading to nearly homogeneous temperatures in the offshore direction. By late summer, warmer advection near the coast relative to that occurring offshore appears to dominate. Warm temperatures are found near the coast; gradients extend hundreds of kilometers offshore. During late fall and winter southward flow begins to increase (Figure 8) and the offshore temperature distribution again becomes nearly homogeneous (Figures 13 and 14).

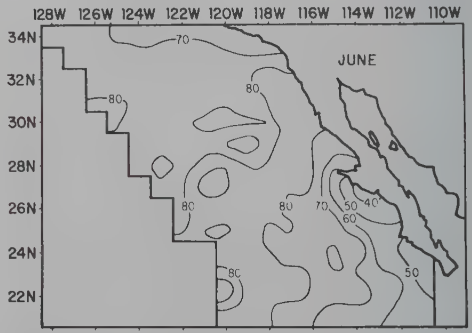


FIGURE 15. Cloud cover during June. Means of reported cloud amounts were computed by 1 degree squares during the month of June. Units are percent of sky obscured.

Cloud Cover

Seasonal and spatial variations in the heat exchange may mask features of upwelling normally evident in distributions of sea surface temperature. In the composite field of total cloud cover for June (Figure 15), Punta Eugenia separates an area of minimum cloud cover along the coast (less than 50%), from an area of maximum cloud cover (greater than 80%). A change in total cloud cover from 40% to 80% could result in a relative decrease of more than 30% in the incident radiation (Seckel and Beaudry, 1973) with corresponding changes in the sea surface temperature.

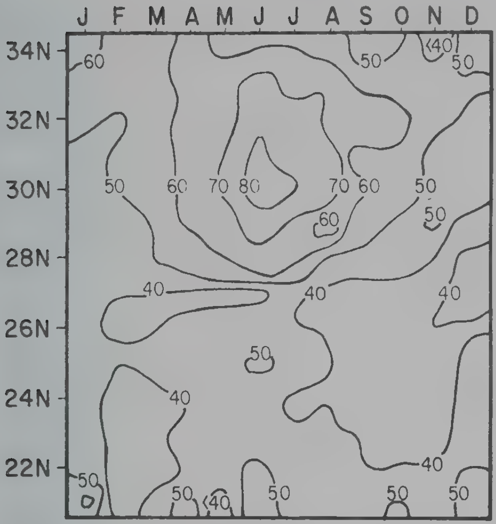


FIGURE 16. Seasonal cycle of cloud cover near the coast. Mean values of reported cloud amounts were computed by month for the group of selected 1 degree squares adjacent to the coast, indicated in Figure 1. Units are percent of sky obscured.

Considering the seasonal variations in cloud cover within the longshore section of coastal squares (Figure 16), maximum cloud cover appears to be associated with the upwelling off Punta Baja, while minimum cloud cover is evident along the entire coast south of Punta Eugenia. When distributions of cloud cover for sections extending westward from the coast are considered (Figures 17 and 18), the section off Punta Eugenia indicates minimum cloud cover at the coast throughout the year, while relative maxima occur at the coast in the Punta Baja section during June and July. The data suggest that differences in the downward flux of radiation associated with these cloud cover distributions could lessen the indications of coastal upwelling in the sea temperature south of Punta Eugenia. To the north, however, the heat flux from the atmosphere during the upwelling season may be insufficient to obscure the effects of cold water upwelled into the surface layer.

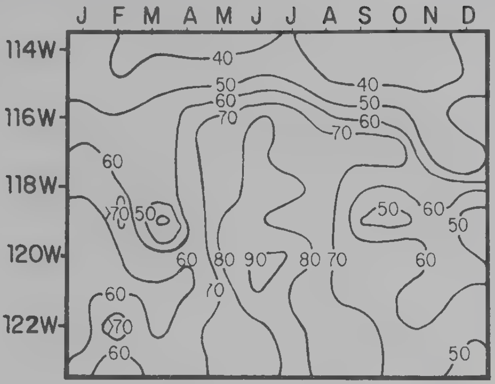


FIGURE 17. Seasonal cycle of cloud cover off Punta Eugenia. Mean values of cloud cover observations were computed by month for the group of selected 1 degree squares extending westward from the coast south of Punta Eugenia, indicated in Figure 1. Units are percent of sky obscured.

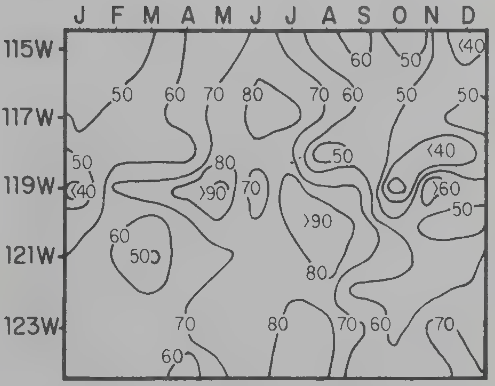


FIGURE 18. Seasonal cycle of cloud cover off Punta Baja. Mean values of cloud cover observations were computed by month for the group of selected 1 degree squares extending westward from the coast south of Punta Baja, indicated in Figure 1. Units are percent of sky obscured.

Wind Stress Curl

Although coastal upwelling occurs only at the ocean boundary, wind-induced upwelling can occur whenever divergence in the surface wind drift is not compensated by other modes of horizontal surface flow. The divergent or convergent nature of the surface Ekman wind drift offshore of the primary coastal upwelling zones is determined by the wind stress curl (Figure 19). If the equatorward wind stress parallel to the coast increases in the offshore direction, a situation characterized by positive curl in the stress field, the offshore component of Ekman transport likewise increases in the offshore direction. The result is continued divergence offshore requiring upwelling to maintain the mass balance. Conversely, if the equatorward longshore wind stress decreases in the offshore direction, the wind stress curl is negative. The result is convergence in the surface wind drift with corresponding frontal formation and downwelling.

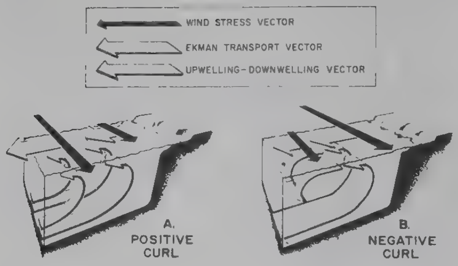

WIND STRESS VECTOR
EKMAN TRANSPORT VECTOR
UPWELLING-DOWNWELLING VECTOR
A. POSITIVE CURL
B. NEGATIVE CURL

FIGURE 19. A conceptual diagram of the relationship of wind stress curl to divergence and convergence of surface Ekman transport offshore of the primary coastal upwelling zone. An increase in the equatorward wind stress parallel to the coast (positive wind stress curl) produces divergence in surface Ekman transport and continued upwelling offshore. A decrease in the equatorward wind stress parallel to the coast (negative wind stress curl) produces convergence in surface Ekman transport and downwelling offshore.

Actual observations of wind stress curl are not available. Alternatively, we have computed the curl of the mean wind stress fields under the assumption that, since the curl is a linear operator, the resulting distributions may resemble mean fields of actual wind stress curl distributions existing off Baja California. Monthly curl fields corresponding to the mean wind stress distributions (Figure 3) were determined (Figure 20). Negative wind stress curl (Ekman convergence) is characteristic of the offshore region. From Punta Baja to Punta Eugenia the convergent region reaches to the coast. The wind stress distributions thus imply favorable conditions for formation of fronts and convergent patches of recently upwelled water in this area. North of Punta Baja and south of Punta Eugenia areas of positive curl (Ekman divergence) extend from the coast to several hundred kilometers seaward. Within these divergent areas there would tend to be a continued, although much reduced, level of upwelling offshore of the primary coastal upwelling zone.

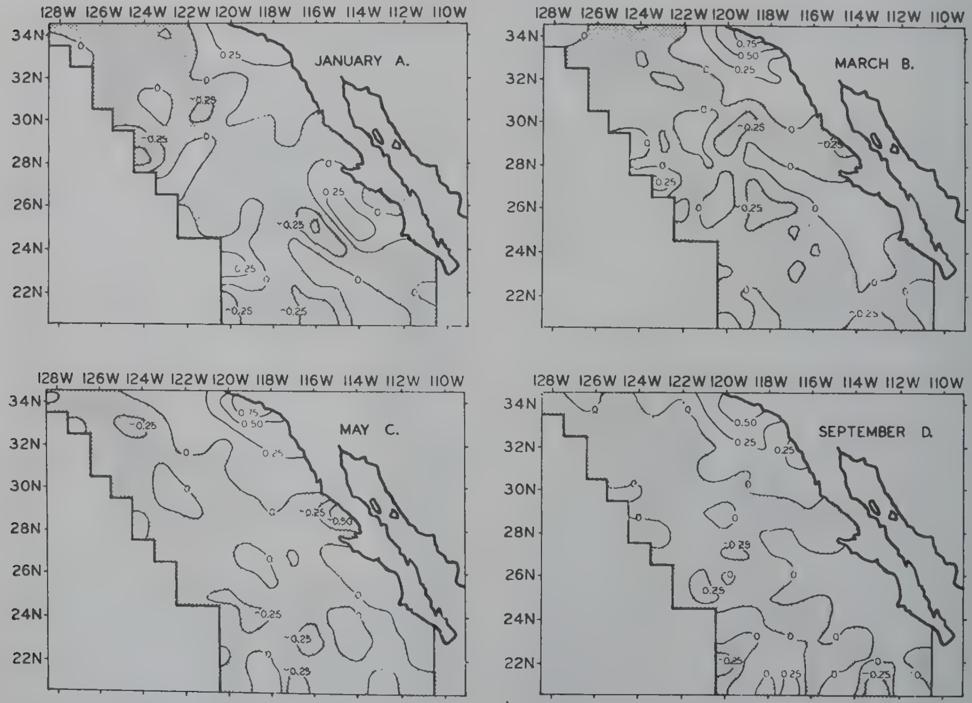

128W 126W 124W 122W 120W 118W 116W 114W 112W 110W
34N 32N 30N 28N 26N 24N 22N
JANUARY A.
MARCH B.
MAY C.
SEPTEMBER D.
0
0.25
-0.25
0.50
-0.50
0.75

FIGURE 20. Wind stress curl. Monthly composite fields of wind stress curl were computed from the surface wind stress fields shown in Figure 3; A. JANUARY, B. MARCH, C. MAY, and D. SEPTEMBER. Units are dynes/cm²/100km. The coutour interval is 0.25 dynes/cm²/100 km. Negative values are shaded.

Munk (1950) has suggested that the poleward undercurrent observed along the California coast may be a consequence of the local wind stress curl. Pedlosky (1974) has indicated theoretically that a poleward undercurrent would be favored by positive wind stress curl along the coast and a poleward decrease in the surface heating. The surface data presented here cannot describe features of the subsurface flow. However the mean wind stress distributions off the coast appear generally consistent with a pattern of countercurrent inshore and equatorward flow offshore, except in the region from Punta Eugenia to Punta Baja where the wind stress curl is not positive. During the fall, the relaxation of upwelling induced equatorward surface flow would favor surfacing of a coastal countercurrent. With these considerations in mind it is interesting to note that indications of a poleward component of ship drift during fall (Figure 9B) are lacking in the region from Punta Eugenia to Punta Baja. Rather, the data suggest separate cyclonic gyres in the regions of positive wind stress curl off the Los Angeles Bight and south of Punta Eugenia.

VARIABILITY AND PERSISTENCE

In addition to responding to the seasonal variations, marine biological communities must also respond to a wide spectrum of environmental variations of time scales ranging from many years to small fractions of a year. A central problem in investigating such fluctuations is the formation of consistent time series of pertinent information.

For any particular synoptic sampling the available reports from ships at sea tend to be sparse and unevenly distributed. In such a situation the variability introduced by random errors in measurement or changes in spatial distribution of reports may be as great or greater than the variability in the process itself. If a definite periodicity is known it may be reasonable to composite corresponding portions of different cycles, as was done in the previous section, in order to obtain an adequate data base. This is not possible in the case of fluctuations which are nonperiodic or where, if they do contain periodic components, the periodicities are undefined.

One way to arrive at fairly consistent time series of wind information with which to investigate fluctuations in upwelling is to make use of analyzed products produced by meteorological agencies. In this section we use 6-hourly computations of offshore Ekman transport based on the synoptic surface atmospheric pressure analyses produced by Fleet Numerical Weather Central. These analyses incorporate all available wind reports in the form of equivalent pressure gradients as well as the available pressure data (Holl and Mendenhall, 1972). Conventional reporting periods correspond to 4AM, 10AM, 4PM, and 10PM Pacific Standard time, yielding four synoptic samplings per day.

Bakun (1973) described a procedure for computing offshore Ekman transport from pressure fields using a geostrophic wind computation and a simplified boundary layer approximation. The results of such computations were called *upwelling indices.* A compilation of daily and weekly means of 6 hourly indices at 15 locations off western North America has been published (Bakun, 1975). The time series discussed in this paper are located at five 3 degree grid intersections, from 21°N to 33°N latitude (Figure 1).

This 3 degree resolution is coarse compared to the 1 degree resolution achieved in the previous section. The pressure fields were originally analyzed on a grid of approximately 3 degree mesh length. Thus any information derived on a smaller scale would consist merely of the details of the particular interpolation function used, rather than having any basis in observed data. Underlying this situation is the fact that the number of reports from the area off Baja California during any synoptic period is only of the order of one per 3 degree square and so analysis of pressure on a smaller scale grid would not increase the resolution of data-based information.

The drag coefficient used in equation (1) to compute these indices was 1.3×10^{-3}. This differs from the value 1.6×10^{-3}, based on the work of Denman and Miyake (1973), used in the previous section. Recent progress in the field of ocean-atmosphere boundary processes suggests that 1.3×10^{-3} may be a more appropriate constant value.

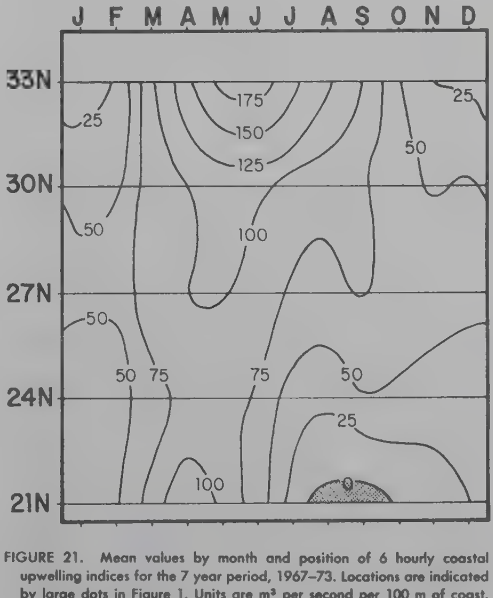


FIGURE 21. Mean values by month and position of 6 hourly coastal upwelling indices for the 7 year period, 1967–73. Locations are indicated by large dots in Figure 1. Units are m³ per second per 100 m of coast. Negative values are shaded.

Actually the drag coefficient appears to vary both with atmospheric stability and with spectral properties of the ocean waves (Davidson, 1974), but the form of the dependencies does not appear well enough established to warrant incorporation of these effects for our purposes. Since the drag coefficient enters linearly into the computations of stress and Ekman transport, the values in the previous section could be adjusted to those of this section by multiplication by the factor $1.3/1.6 = 0.8125$. Because of such uncertainties, these results, although yielding reasonably realistic numerical values, should properly be viewed as being "uncalibrated" in terms of absolute quantitative detail. The uncertainty in magnitudes is more severe in the case of indices computed from analyzed pressure fields.

Comparison of the 7 year (1967–73) mean values of the 6 hourly upwelling indices (Figure 21) to the seasonal cycle of offshore Ekman transport composited on a 1 degree basis from actual ship reports (Figure 6) illustrates the smoothing of gradients and other spatial details on the 3 degree synoptic index format. It also illustrates a severe spatial distortion in absolute magnitudes discussed by Bakun (1973) which results in amplification of the computed indices at 33°N latitude relative to those at points further south. The figures in this paper which display absolute magnitudes of computed upwelling indices are intended to indicate temporal variations, i.e. relationships along the horizontal axis of the figures. Contours are connected between different locations only as a visual aid and to indicate variations in seasonal timing between different locations. Comparisons of absolute magnitudes on the vertical axis can be misleading. In the case of normalized properties such as skewness and kurtosis the problem is less severe.

Properties of Fluctuations

High variance in the 6-hourly computed indices tends generally to correspond in season and location to high mean value (Figure 22). Thus the winter season is characterized by a generally relaxed level of activity and thus a more stable upwelling regime. Two variations from the pattern are noticeable. At 21°N latitude where during late summer the mean goes negative, i.e. downwelling occurs on average, there is a relative maximum in the variance. Thus the low mean absolute values must reflect a near cancellation of contributions to the variance by large positive and negative fluctuations. Off central Baja California where there are double peaks in the mean, the larger occurring in spring and the lesser in late summer, the late summer period exhibits the greater variance.

Skewness of the monthly distributions is generally positive (Figure 23). Thus the strong departures from the mean are most often spikes of even more intense upwelling separated by longer relaxed periods rather than an equal mix of fluctuations above and below the norm. Highly skewed distributions are at 21°N latitude during the spring

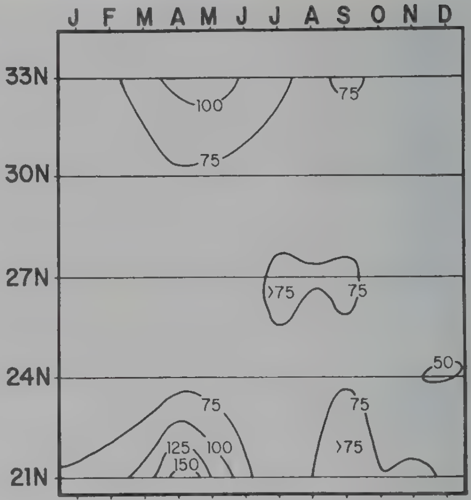


FIGURE 22. Standard deviations of monthly distributions of 6 hourly coastal upwelling indices. Locations are indicated by large dots in Figure 1. Units are m³ per second per 100 m of coast. Period covered is 1967–73.

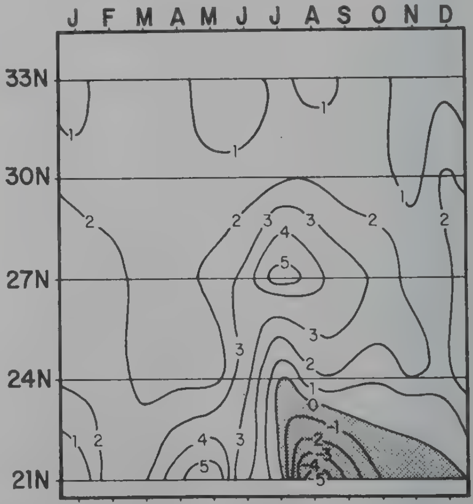


FIGURE 23. Skewness of monthly distributions of 6 hourly coastal upwelling indices. Locations are indicated by large dots in Figure 1. Period covered is 1967–73. Negative values are shaded.

upwelling maximum and off Central Baja California during the relative minimum which separates the spring and late summer maxima. The skewness turns negative during late summer and fall at 21°N. The area of negative skewness extends to 24°N during July and corresponds to a similarly shaped region of low mean monthly values of the indices (Figure 21). This situation appears to be one of fairly consistent low level upwelling interrupted at infrequent intervals by downwelling events of such an intensity as to nearly cancel the upwelling on average. The mean actually goes negative at 21°N during August and September. These downwelling events probably reflect the occurrence of tropical storms.

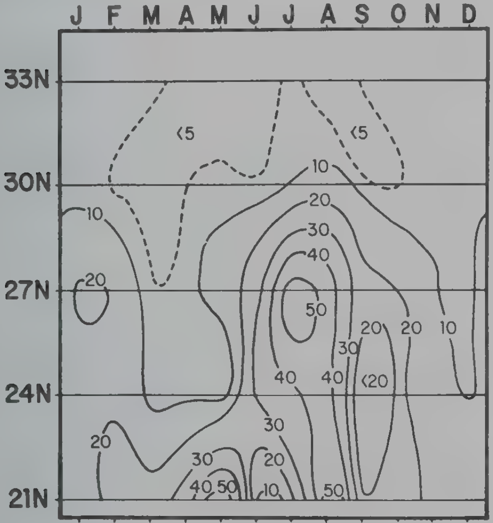


FIGURE 24. Kurtosis of monthly distributions of 6 hourly coastal upwelling indices. Locations are indicated by large dots in Figure 1. Period covered is 1967–73.

Kurtosis of the monthly distributions is greater than 3.0 at all months and locations indicating larger contributions from extreme events than would be the case in a Gaussian process (Figure 24). Off central and southern Baja California during spring and summer the large variance corresponds to large kurtosis, again indicating the importance of rare, very intense events. In the north the spring and fall seasons of maximum variance are characterized by minimum kurtosis, indicating the variance to be dominated by more frequent, less extreme pulsations.

Power spectra (Figure 25) were selected as being representative of a number of similar spectra computed for various segments of the 7 year series of 6 hourly indices. The major features, i.e., the strong diurnal peak and a general increase in energy at low frequencies representing seasonal and other long term variations, appear consistently. The indication of a major amount of energy spread over an "event scale" of periods ranging from 2 or 3 days to several weeks is also typical. The spectral peak at the semidurnal frequency reflects the non-sinusoidal shape of the diurnal fluctuation which tends to have a faster rate of change during the morning to afternoon increase than during the evening to morning relaxation.

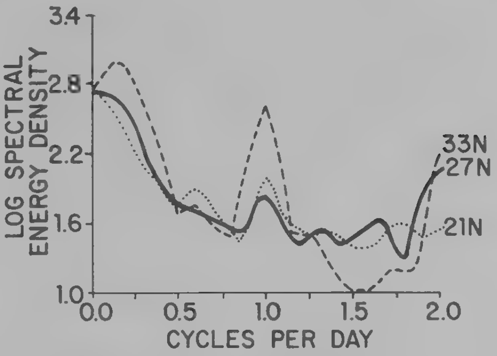


FIGURE 25. Power spectra of 6 hourly coastal upwelling indices. Spectra are plotted for time series at three locations (21°N, 107°W; 27°N, 116°W; 33°N, 119°W) for the period February 27 through July 1, 1972.

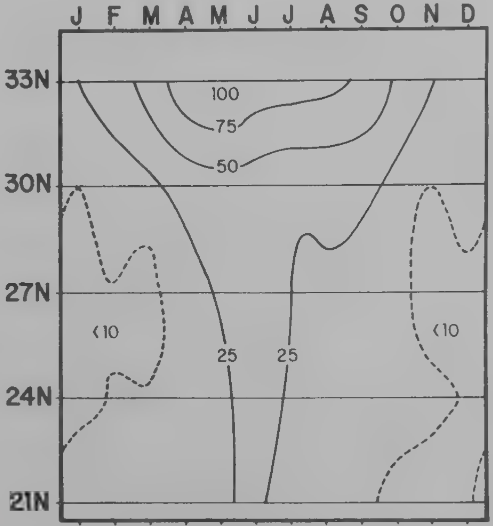


FIGURE 26. Diurnal variation in upwelling indices. Mean differences between upwelling indices computed from the 4 PM Pacific Standard Time synoptic sampling and those computed from the 10 AM sampling 6 hours earlier were computed by month at locations indicated by large dots in Figure 1. These two sampling periods tend to be extremes of the diurnal cycle as resolved by these data. Units are m³ per second per 100 m of coast. Period covered is 1967–73.

The 10AM and 4PM (Pacific Standard Time) synoptic periods tend to be the extremes of the diurnal cycle as well as it can be resolved with the four samples per day available. The mean difference, the afternoon value minus the morning value, is positive at all months and locations (Figure 26). The amplitude tends to be greatest in the late spring and early summer and least in the winter. At 21°N latitude the minimum is earlier than at the locations further north, occuring during the fall. The diurnal variation is greatest at 33°N and is progressively smaller to the south. How much of this apparent north-south gradient in the diurnal effect may be due to the previously mentioned spatial distortion is presently unclear.

The diurnal effect is very apparent in autocorrelation functions produced from upwelling index time series (Figure 27), where the diurnal rise and fall appears superimposed on a strong decline in autocorrelation which occurs within 1 to 2 days. This rapid decline illustrates the characteristically short time scales of the indicated pulses of upwelling producing wind stress.

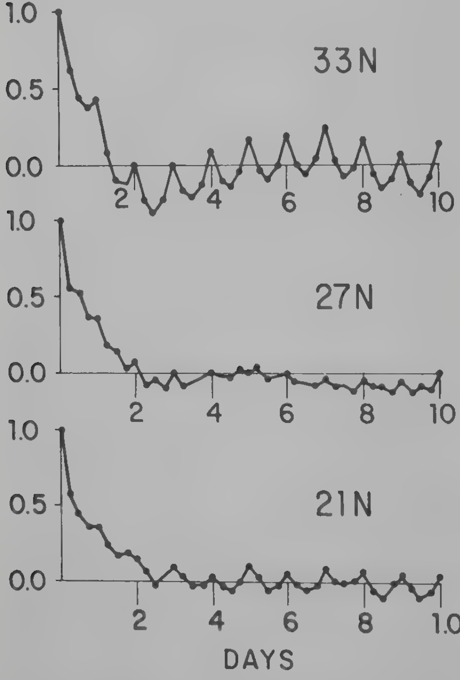


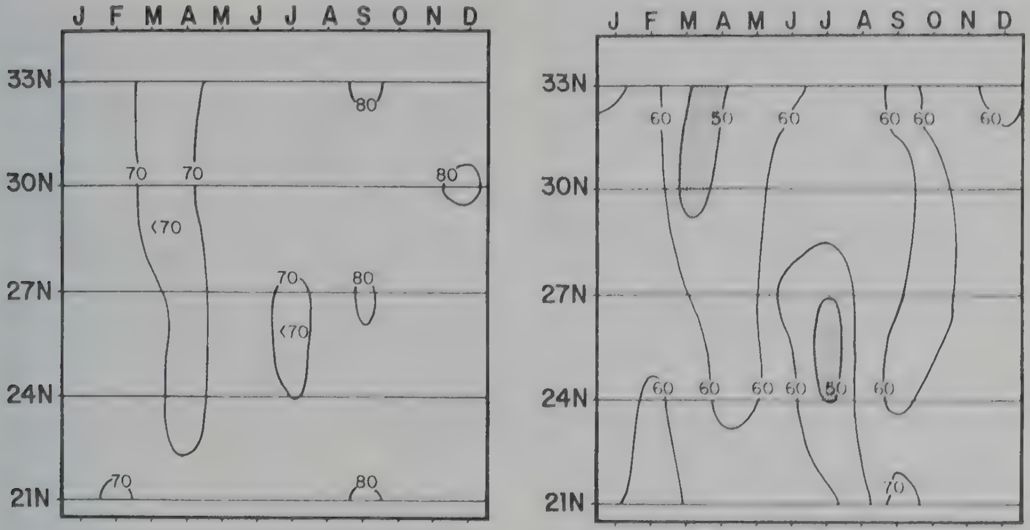
FIGURE 27. Autocorrelation functions for 6 hourly coastal upwelling indices. Functions are plotted for three locations (21°N, 107°W; 27°N, 116°W; 33°N, 119°W) during the period February 27 through July 1, 1972.

Persistence

Characteristic time scales were further examined in terms of persistence of anomalies in the 6 hourly upwelling indices (Figure 28). Since anomalies in these series tend to be much larger than the differences between various types of fits to the annual cycle, mean seasonal values were simply defined by linear interpolation between succeeding months, the midpoints of which were assigned the 7 year composite mean monthly value of the 6 hour upwelling indices. To avoid complicating effects of the diurnal cycle the analysis was done in terms of daily means. An anomaly was defined as the difference between a daily mean value and the value for the particular day from the linearly interpolated mean annual cycle. The percentage of times during the 7 year time series that a daily anomaly had the same sign as the anomaly for the previous day was computed for each month and location (Figure 28A). Situations where the anomaly was so small that it was not significantly either positive or negative were rejected by requiring the previous anomaly to have an absolute value of at least 10 m^3 per second per 100 m of coastline for the particular day to be used in the computation. This process was repeated using the respective anomalies 2, 3, and 5 days earlier in the comparisons (Figure 28B, C, and D).

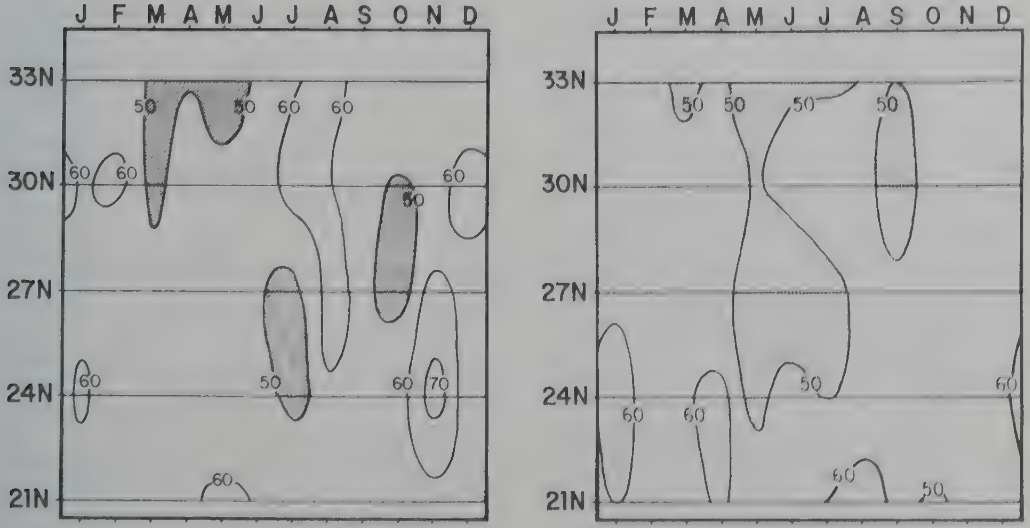
The daily anomaly has the same sign as the previous day's anomaly about 70 to 80% of the time depending on month and location (Figure 28A). By the second day (Figure 28B) the persistence of sign has dropped below 50%, indicating no tendency for persistence, at some months and locations. After 5 days, the months and locations where the anomaly is below 50% are considerably greater in number than those where it is greater than 60%. Thus any persistence of individual wind stress events on scales greater than 5 days appears to be slight.

In examining these series, however, one notices a certain persistence on longer scales which is evident in groupings of individual events resulting in general levels of average intensity above or below the seasonal norm. To illustrate this a similar analysis was performed on monthly anomalies. In order to have access to a longer data series for such a monthly analysis we have used a series computed from monthly mean pressure fields which extends back to 1946. Bakun (1973) has shown that indices computed in this manner correlate highly with corresponding series of monthly means of 6 hourly indices. In order to have a value 5 months previous to our first data point for comparison, we begin with June, 1946, and then work through the following 28 years ending May, 1974. The resulting distributions (Figure 29) are somewhat more noisy than those produced from the daily series (Figure 28) because there are only 28 data points for each month and location compared to the 200 or more data points per month and location in the 7 year daily series. A level of persistence of



A. 1 DAY EARLIER

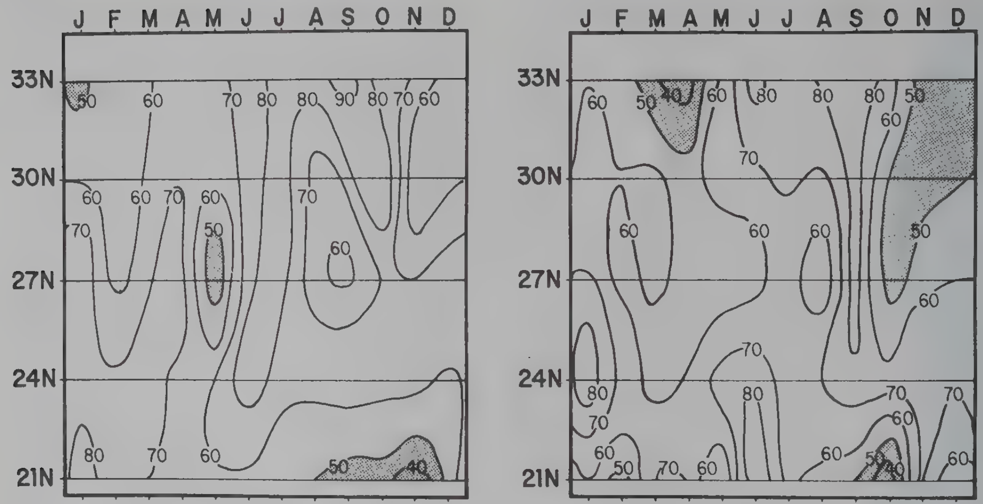
B. 2 DAYS EARLIER



C. 3 DAYS EARLIER

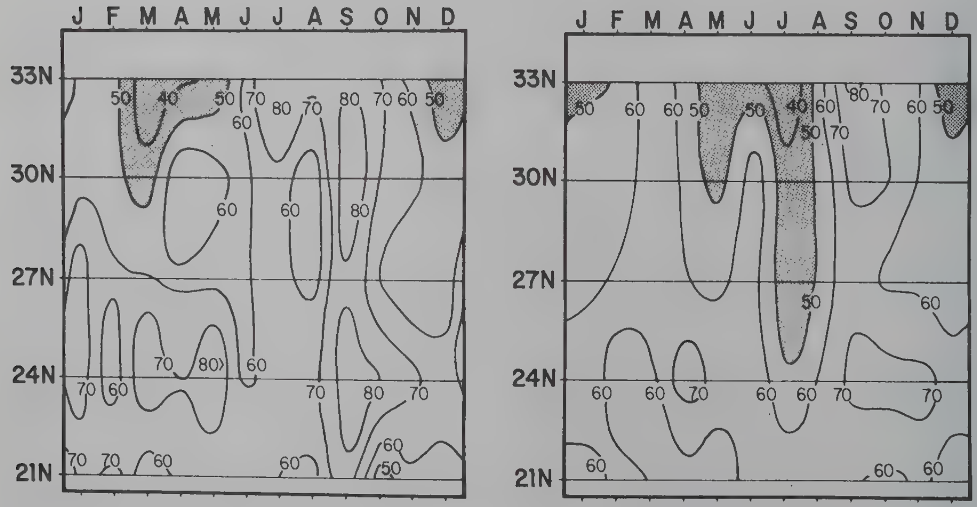
D. 5 DAYS EARLIER

FIGURE 28. Percentage of daily upwelling index anomalies having the same sign as the daily anomaly. A. 1 day earlier, B. 2 days earlier, C. 3 days earlier, D. 5 days earlier. A daily anomaly is defined as the difference between the daily average of 6 hourly coastal upwelling indices and the characteristic value for that day derived from the long term mean annual cycle. Period covered is 1967–73. Shading indicates percentages less than fifty



A. 1 MONTH EARLIER

B. 2 MONTHS EARLIER



C. 3 MONTHS EARLIER

D. 5 MONTHS EARLIER

FIGURE 29. Percentage of monthly upwelling index anomalies having the same sign as the monthly anomaly, A. 1 month earlier, B. 2 months earlier, C. 3 months earlier, D. 5 months earlier. A monthly anomaly is defined as the difference between a monthly upwelling index value and a 20 year (1948–1967) mean value for the particular month. Period covered is June, 1946 through May, 1974. Shading indicates percentages less than fifty.

monthly anomalies after 5 months (Figure 29D) roughly equivalent to that for daily anomalies after 5 days (Figure 28D) is indicated.

One simple feedback system which may contribute to persistence of levels of upwelling intensity beyond the duration of individual upwelling events is as follows. An upwelling event or combination of events is eventually reflected in cooler water at the sea surface. This increases the temperature gradient in the lower atmosphere between the continent and the ocean, which in turn increases the onshore-offshore atmospheric pressure gradient. The result is greater longshore wind stress which feeds back to the upwelling process, transmitting an underlying level of intensity from one event to another. Whatever the major mechanism may be, these results suggest that general levels of upwelling intensity above or below the seasonal norm have a tendency to be persistent over periods approaching the seasonal time scale.

Spatial Coherence

Finally, an analysis using a spatial lag rather than a temporal lag, can yield some insight into the spatial coherence of upwelling anomalies. The percentage, by month and location, of daily anomalies having the same sign as the corresponding daily anomaly at 27°N latitude was determined (Figure 30). Again, we have required that the anomaly at 27°N be at least 10 $m^3/sec/100$ m of coast for it to be considered significant. The percentage at 27°N is of course always 100%. The percentage drops off more rapidly to the south than to the north. In fact at 21°N latitude it actually drops below 50% during September indicating the anomaly had a sign opposite to that at 27°N more often than not. In total, the indication is that coherence of upwelling anomalies over regions the size of the coast of Baja California is not necessarily to be expected.

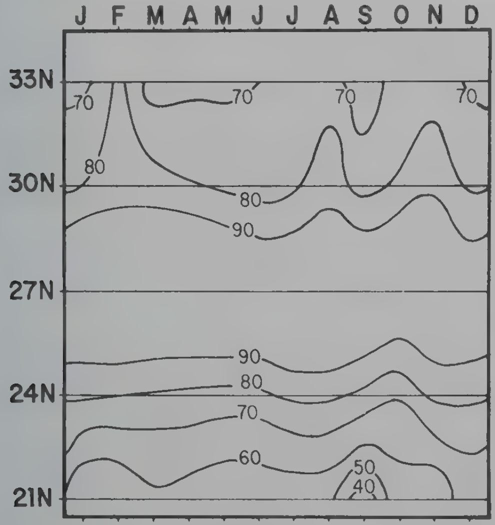


FIGURE 30. Percentage of daily upwelling index anomalies having the same sign as the corresponding daily anomaly at 27°N. Period covered is 1967–73. Shading indicates percentages less than fifty.

UPWELLING OFF BAJA CALIFORNIA DURING RECENT YEARS

We now attempt to characterize the upwelling situation off Baja California since 1972. Bakun (1973) presented coastal upwelling indices based on monthly mean data for the period 1946 through 1971. These are intended to represent the primary coastal divergence mechanism (Figure 2). These series were updated through July 1977 (Table 1) at 5 locations off southern California and northern Mexico (Figure 1). In computing these monthly indices a higher drag coefficient, 0.0026, was employed to roughly compensate for the underestimate of the stress caused by using mean data in the nonlinear calculation involved in equation (1).

In the section on the seasonal cycles we described the effect of the curl of the wind stress in causing convergence or divergence in the surface layer outside of the immediate coastal upwelling zone (Figure 19). This effect is probably important biologically. For example, certain organisms may be favored by a situation where the surface layer continues to diverge, on average, offshore of the coastal upwelling zone. Nutrients would continue to be fed into the surface layer, planktonic grazers swept away, etc. Other organisms may depend on concentration in convergent frontal zones of the organic material produced as a result of the upwelling near the coast. These might be favored by strong coastal upwelling in conjunction with or followed by strong offshore convergence.

In order to have an indicator of this effect, a set of indices of divergence of the Ekman transport field outside of the immediate coastal upwelling region was generated for the same locations and from the same monthly mean pressure fields as were the monthly coastal upwelling indices. The applicable equation is derived by Fofonoff (1963):

$$\nabla \cdot \vec{V}_E = \frac{1}{f}(\nabla \chi \vec{\tau}) \cdot \vec{k} - \frac{\beta}{f}\vec{V}_E \cdot \vec{j} \qquad (3)$$

where:

$\nabla \cdot \vec{V}_E$	represents the divergence of Ekman transport
$(\nabla \times \vec{\tau}) \cdot \chi$	represents the vertical component of the curl of the wind stress
f	is the Coriolis parameter
β	is the meridional derivative of f,
$\vec{V}_E \cdot \vec{j}$	is the meridional component of Ekman transport.

The stress and Ekman transport inputs to equation (3) were computed as for the monthly mean upwelling indices. Numerical values were assigned as vertical velocities required to balance the computed divergences (Table 2).

During the early months of 1972, coastal upwelling appears to have been generally stronger than normal (Figure 31). This was accompanied by anomalous offshore convergence except in the extreme south where anomalous offshore divergence tends to be a persistent feature (Figure 32). Late summer and early fall of 1972 are characterized by lower than normal coastal upwelling index values except during September in the southern portion of the region. The month of December shows stronger than normal upwelling index values along the whole coast. An anomalously divergent situation is indicated offshore during November and December.

TABLE 1

Monthly coastal upwelling indices *

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
					1972							
33N	8	33	168	228	243	283	254	201	144	36	16	24
30N	91	88	186	180	165	168	125	113	90	61	67	85
27N	120	138	199	236	197	162	101	58	94	64	77	81
24N	85	77	161	197	179	156	53	12	84	24	59	45
21N	86	86	128	117	74	97	5	−1	13	1	38	26
					1973							
33N	15	1	182	216	290	282	288	234	167	65	75	24
30N	65	7	178	193	155	178	137	149	121	90	93	97
27N	105	28	173	181	148	138	90	115	138	106	117	97
24N	68	34	155	142	142	107	55	83	122	84	106	72
21N	39	52	163	116	108	83	16	10	27	8	19	33
					1974							
33N	1	43	91	207	372	330	229	245	159	97	26	4
30N	22	104	93	234	284	263	147	167	141	104	74	34
27N	56	105	123	208	208	160	67	116	94	80	60	39
24N	52	78	100	138	147	82	24	50	53	54	43	57
20N	31	60	81	53	125	22	4	1	4	−1	5	37
					1975							
33N	10	45	123	197	282	362	322	251	166	100	55	16
30N	50	62	127	174	187	197	192	194	180	146	134	58
27N	43	84	127	183	165	161	99	115	117	133	99	40
24N	45	85	133	185	130	93	37	46	50	96	56	35
21N	19	47	41	75	100	28	2	−1	−8	6	28	26
					1976							
33N	−1	34	120	198	304	262	277	212	88	50	4	−6
30N	44	64	139	160	231	199	160	145	70	80	54	28
27N	27	51	127	158	215	214	142	170	57	58	28	17
24N	24	50	127	153	191	172	107	86	57	72	34	32
21N	21	33	122	125	119	36	30	4	1	16	18	35
					1977							
33N	9	57	163	207	224	325	285					
30N	38	131	201	169	182	222	181					
27N	10	110	189	206	224	252	135					
24N	23	96	153	194	184	163	79					
21N	83	92	230	192	260	134	70					

* Units are cubic meters per second per 100 m length of coast. Values signify volume transported offshore in the surface Ekman layer.

TABLE 2

Monthly Surface Layer Divergence Indices*

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
					1972							
33N	280	15	242	-195	-328	-465	-689	-155	-218	-31	204	211
30N	97	-326	-434	-627	-651	-801	-687	-458	-408	-154	96	76
27N	-240	-236	-584	-88	-217	-232	-157	-82	-168	42	-1	82
24N	-197	-126	-255	-167	-310	-112	-10	-43	3	-24	-19	5
21N	471	354	380	321	371	303	97	9	138	29	172	87
					1973							
33N	68	-9	267	100	-367	-130	-231	-73	-45	126	119	260
30N	-6	-23	-299	-461	-892	-924	-770	-652	-726	-338	-359	63
27N	-31	-63	-165	-186	-225	-220	-239	-157	-208	-52	-124	90
24N	27	-97	-181	-189	-265	-236	-177	-62	65	22	-23	12
21N	36	152	-43	32	88	163	1	119	133	90	155	195
					1974							
33N	25	375	-103	187	-387	-651	-334	-506	-81	-69	241	310
30N	-22	18	-338	-591	-969	-903	-590	-907	-556	-385	3	151
27N	-67	-49	-118	-136	-207	-135	-45	-112	61	114	116	-65
24N	-8	-81	-121	-103	-203	-131	33	-66	30	-23	-20	-138
21N	141	135	-43	103	25	126	7	-6	88	69	140	274
					1975							
33N	390	30	-9	-65	-387	-1116	-709	-651	-73	129	416	312
33N	189	-204	-332	-503	-909	-1223	-741	-832	-535	-379	46	71
27N	-10	-65	-106	-200	-256	-350	-309	-149	-28	-45	111	15
24N	-111	-127	-160	-91	-166	-163	-163	-88	-64	-94	-37	-40
21N	97	150	135	119	13	20	-13	8	91	131	245	186
					1976							
33N	393	206	376	-64	-201	-277	-350	-570	-30	123	246	230
30N	128	-52	-180	-643	-1097	-1021	-1009	-975	-345	-155	110	111
27N	25	-26	-192	-169	-227	-311	-332	-279	-40	71	142	41
24N	-93	-55	-144	-4	-155	210	-4	41	64	-64	-44	-83
21N	223	215	486	573	553	389	368	128	109	357	413	489
					1977							
33N	230	315	317	-111	-160	-827	-493					
30N	98	-12	-470	-787	-982	-1557	-1155					
27N	72	157	-75	-416	-449	-681	-269					
24N	-137	-5	-217	-409	-218	-131	-27					
21N	668	719	289	382	-312	95	228					

*Values signify vertical velocities at the bottom of the Ekman layer required to balance the indicated divergence or convergence occurring offshore of the primary coastal upwelling zone. Units are millimeters per day, positive upwards.

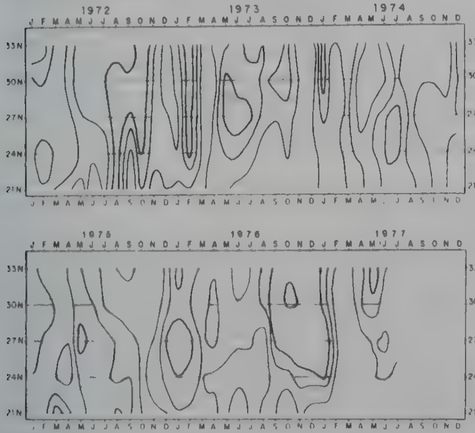


FIGURE 31. Monthly coastal upwelling index values (Table 1) in terms of quartiles of the frequency distribution made up of all values for the given location and calendar month within the 1946–77 time series. Quartiles are delineated by contours. The two quartiles below the median are shaded.

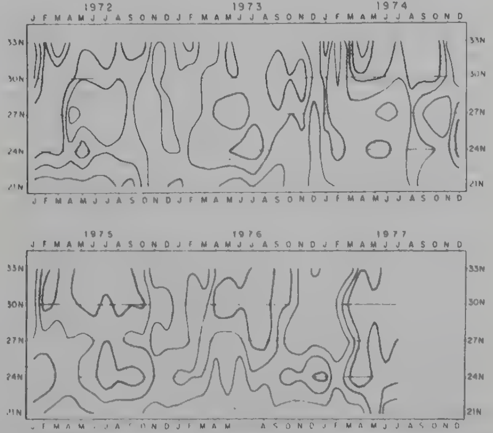


FIGURE 32. Monthly offshore surface layer divergence indices (Table 2) in terms of quartiles of the frequency distribution made up of all values for the given location and calendar month within the 1946–77 time series. Quartiles are delineated by contours. The two quartiles below the median are shaded.

Weak coastal upwelling is indicated off Baja California in February followed by higher than normal intensity during March and April (Figure 31). In the north a low tendency prevailed from May through October coupled with greater than normal offshore convergence. At 21°N latitude the coastal upwelling indices were anomalously high all year, becoming extremely anomalous late in the year. Extreme values appear all along the coast during November and December. The indication of high offshore divergence which is a persistent feature at 21°N during the recent period spreads northward along the whole coast during December (Figure 32).

An alternating pattern off northern Baja California was evident during early 1974 with a low upwelling index anomaly in January, a high anomaly in February, a low in March, and very high values in April and May. Low values appear in the south central region during June and July. The northern area is characterized by anomalous offshore convergence from May through October.

Generally higher than normal coastal upwelling is indicated during March 1975, followed by a period of lower than normal intensity which lasts until May in the north, but continues generally through the summer in the south. The latter portion of 1975 exhibits higher than normal coastal upwelling index values. The offshore region appears to have been anomalously convergent, particularly during summer and early fall (Figure 32).

A period of weak coastal upwelling is indicated during early 1976, followed by stronger than normal upwelling during the summer. The fall and winter are characterized by lower than normal upwelling index values as far south as 24°N latitude. The offshore divergence index values indicate anomalous convergence in the north during spring and summer of 1976, and anomalous divergence during late fall.

During the final revision of this paper, index values were available for the first 7 months of 1977. Coastal upwelling index values are generally above average except during January and during May in the north (Figure 31). Offshore divergence index values are high during January and February, but anomalously low during spring and early summer (Figure 32).

Offshore divergence index values at 21°N tend to be very high in this recent 6 year period relative to the values in earlier years of the time series (Figure 32). Whether this reflects a real longer period variation in the wind pattern is not clear at this time. Changes in the distribution of available data or in the meteorological analysis procedures may be affecting the computed values. In general, care should be exercised in attempting to discern long term trends using this type of index series. Rather, the purpose is to provide a useful indication of relative variations within groups of fairly contemporaneous years.

CONCLUDING REMARKS

In our descriptions of seasonal features, the summaries by 1 degree squares indicated significant spatial variations on scales smaller than the 3 degree resolution we can achieve in synoptic indices. Relating the large scale indices to smaller scale features may require the "engineering approach" suggested by Smith (1968) where one looks at the "outputs," in our case physical or biological data on a smaller scale in those particular instances where it is available from research cruises, shore stations; etc., and the larger scale synoptic "inputs" and attempts to define the "transfer functions." As a first approximation it may be reasonable to assume, for example, that where greater than normal convergence is indicated on the larger scale, smaller scale divergences which exist might weaken and convergences strengthen.

We are continuing to assemble pertinent data including ocean-atmosphere heat exchange components, dynamic topographies from hydrographic data, sea level records, mixed layer depths, temperature series from shore stations, river runoff records, etc. We are looking into possibilities of satellite inputs and are in the process of expanding our wind stress indices to lower latitudes using newly developed "global band" atmospheric products (Lewis and Grayson, 1972).

Our plans for the future include computer modelling of some of the processes controlling the fishery environment. It is sometimes the case in fishery oceanography that rather than having too little detail in our environmental descriptions we have too much, and very little means to integrate it into a total "environmental condition" which will make sense in terms of a total fishery. Modelling, rather than creating any new data, may help to distill the various data available down to a useable number of significant factors, the year to year variations of which could be quantitatively compared. Time series of these factors might be generated from historical data and related to the past history of fishery stocks. Continuous operational updates could than perhaps provide practical environmental inputs for systems approaches to fishery management.

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7804

SKIPJACK TUNA, *KATSUWONUS PELAMIS*, HABITAT BASED ON TEMPERATURE AND OXYGEN REQUIREMENTS

Richard A. Barkley,[1] William H. Neill,[2] and Reginald M. Gooding[1]

ABSTRACT

The habitat of skipjack tuna, *Katsuwonus pelamis*, has generally been assumed to be the warm surface layers of tropical and subtropical ocean, where most of these fish are seen and caught. But experiments with captive Hawaiian skipjack tuna imply that their habitat is more restricted, with boundaries defined by both temperature and dissolved oxygen. The lower temperature limit appears to be about 18° C. The upper temperature limit apparently varies with size of the fish, from 30° C or more for small individuals to as little as 20° C for the largest. Skipjack tuna also require water with unusually high concentrations of dissolved oxygen, at least 3.0-3.5 ml/l (4-5 ppm), for long-term survival. If our Laboratory findings with captive skipjack tuna accurately define their natural habitat, only the smallest of these animals can inhabit the warm surface waters of the tropics; those larger than 4-5 kg must inhabit the thermocline. Our hypothesis, which can be tested, explains many features of the known distribution of skipjack tuna in the eastern and central Pacific Ocean.

For skipjack tuna, *Katsuwonus pelamis* (Linnaeus), the question "Where are the fish?" is particularly hard to answer. Their habitat is known only in the most general terms. These fish are found in tropical and subtropical waters of all oceans, at surface temperatures between 15° and 30° C. Because they are caught most frequently by methods such as trolling, purse seining, and pole-and-line fishing, it is generally assumed that skipjack tuna inhabit the surface mixed layer. Japanese longline gear, which fishes well below the sea surface, catches very few skipjack tuna, and then only on the hooks which fish nearest the surface (Yabe et al. 1963). In a review of the literature on this species, Matsumoto and Skillman[3] pointed out that the sea-surface temperature range where most skipjack tuna are caught varies from one fishery to another. Off Tasmania and southeast Australia, the range is 15° to 18° C. Off Japan and South America, the range appears to be 20° to 24° C, while the fishery off southern India operates in water of 28° to 29° C. The Hawaii fleet fishes skipjack tuna all year, in water with surface temperatures ranging from 23° to 27° C, with the majority of catches in the warm, summer months.

Because studies of the occurrence of wild skipjack tuna in relation to sea-surface temperature yield such disparate results from one area to another, and because the total temperature range, 15° to 30° C, includes more than half of the surface area of the world's oceans, we have worked with captive animals in a series of experiments intended to define more precisely their physiological requirements. Results of three of these studies (Neill et al. 1976; Dizon et al. 1977; Gooding and Neill[4]) provided information on the skipjack tuna's temperature and dissolved oxygen requirements which, taken together, appear to define the actual habitat of this species in nature.

We present here a summary of the physiological studies and their results, which suggest specific temperature and dissolved oxygen values that define the spatial limits of the skipjack tuna habitat. With the resultant temperature and dissolved oxygen values, we have mapped the habitat of the skipjack tuna using averaged oceanographic data from the eastern Pacific Ocean.

These habitat maps present our hypothesis in a testable form. If skipjack tuna in nature have the same requirements as those studied in captivity, their distribution should, on average, correspond

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[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

[2] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii; present address: Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843.

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with the habitat volume shown on the maps. If, under normal oceanographic conditions, they occur in significant numbers well outside of the mapped habitat volume the hypothesis is invalid, and we should look for evidence of adaptations (behavioral, physiological, and genetic) which were not evident in our work with captive fish. If the distribution of skipjack tuna is more restricted than our habitat maps would indicate, we should look for factors in addition to temperature and dissolved oxygen (e.g., turbidity) which might further limit the habitat. Salinity is not apt to be one of these factors, however, since captive skipjack tuna do not respond to rather drastic changes in this variable (Dizon 1977).

More immediate and definitive tests of the hypothesis can be made by tagging wild skipjack tuna of various sizes with tags capable of sensing and telemetering depth, temperature, and dissolved oxygen.

TEMPERATURE AND OXYGEN REQUIREMENTS

Lower Temperature Limit

Dizon et al. (1977) determined that 15° C was the lower lethal temperature limit for skipjack tuna. They subjected recently caught, apparently healthy individual fish to water temperatures which decreased 1° or 5° C/day, starting at ambient temperature (about 24° C), with other skipjack tuna held continuously at ambient temperature as controls. All seven of the test animals survived and fed until temperature had declined to 18° C; at 17° C all but one fish stopped eating, and one fish died. None of the fish survived 15° C for more than a few hours. Accordingly, we have selected 18° C as the lowest water temperature which Hawaii skipjack tuna can withstand for prolonged periods of time without significant increases in mortality.

This preliminary estimate of the lower temperature limit is essentially identical with the value obtained by Williams (1970) from a comparison of fishery catch data with sea-surface temperatures in the eastern Pacific. Williams found that most skipjack tuna were caught in water with temperatures between 29° and 20° C, with diminishing catches down to temperatures between 18° and 17° C, and no catches in colder waters.

Three large (ca. 70 cm) Hawaiian skipjack tuna released with tags that telemetered swimming depth were found to spend >85% of their time in water warmer than 20° C and <10% in water colder than 18° C (Dizon et al. in press).

In the western South Pacific, skipjack tuna have been caught in water near 15° C, off Tasmania (Robins 1952) and off eastern Australia (G. I. Murphy, Division of Fisheries and Oceanography, CSIRO, New South Wales, Australia, 1977, pers. commun.). These fish probably belong to a different subpopulation (Fujino 1972) than fish found in Hawaii.

Lower Dissolved Oxygen Limit

Gooding and Neill (see footnote 4) examined the effects of low dissolved oxygen concentrations on skipjack tuna. Their animals, habituated in open tanks with circulating, essentially saturated seawater (4.5 ml O_2/l, or 6.4 ppm), were transferred to tanks in which the concentration of dissolved oxygen could be maintained at a preselected constant subsaturation level. Temperatures in both sets of tanks were ambient, 23° to 24° C. Dissolved oxygen concentrations down to 1.0 ml/l (1.4 ppm) were used. Resistance times and swimming speeds were measured, and general behavior was observed for up to 4 h in each experiment. Under their experimental conditions, Gooding and Neill concluded that hypoxic stress was first manifest, through changes in swimming behavior and speed, at about 2.8 ml/l (4.0 ppm), a value fairly typical for fish. Lethal oxygen levels, leading to death in 4 h or less, were found to be higher than those for any other freshwater or marine fish thus far studied. Only one fish (out of six) survived 4 h at 2.5 ml/l (3.5 ppm), and none survived as long as 2 h at still lower concentrations. At higher oxygen values, above 2.5 ml/l, all skipjack tuna tested in this study survived at least 4 h.

Because we sought to estimate the lowest dissolved oxygen concentrations that skipjack tuna can tolerate indefinitely without significant stress, we have chosen a conservative value of 3.5 ml/l (5 ppm) as the lower limit to the skipjack tuna's habitat, where temperature and other variables are not limiting.

Upper Temperature Limit

The case for an upper temperature limit to the skipjack tuna's habitat is somewhat less direct. Three small (30-35 cm) individual skipjack tuna maintained in water warmed 1°C/day survived until the temperature reached 33° C, when two died; the other lived until the water reached 34° C (Dizon et al. 1977). Skipjack tuna have a high metabolic rate and a countercurrent heat exchanger in their circulatory system which dramatically restricts heat loss through the gills. This accounts for the fact that freshly caught wild skipjack tuna can have red muscle core temperatures as high as 11° C above that of the surrounding water (Stevens and Fry 1971).

Temperature excesses of this magnitude could lead to dangerously high muscle temperatures if they occur in the warmer parts of the ocean. To examine this possibility we use a heat balance model developed for skipjack tuna by Neill et al. (1976) which yields an estimate of temperature excess in the red muscle core as a function of size and metabolic activity (Figure 1a). Actual muscle core temperatures are found by adding the values shown in this figure to the temperature of the surrounding water, for any given size fish. Clearly, large skipjack tuna in surface waters of the tropics must either tolerate high muscle core temperatures, or reduce their metabolic activity substantially below the 3 mg O_2 g^{-1} h^{-1} level.

But skipjack tuna appear to avoid heating their muscle tissue much above 35° C (Stevens and Fry 1971). This upper limit must place a similar upper limit on the water temperatures which skipjack tuna can inhabit, unless they can thermoregulate physiologically or behaviorally. In Figure 1b, 35°C is taken as the upper limit for the red muscle core, and temperature excesses of Figure 1a are subtracted from that value to arrive at an estimate of the upper temperature limits for the habitat of skipjack tuna, as a function of size. If the values thus obtained are valid, these fish should be able to live anywhere in the ocean when they are small, but they should be limited to lower and lower environmental temperatures as they grow. The largest known skipjack tuna, weighing approximately 16 kg, would—if active enough—be confined to water temperature near 18°C, which is also their approximate lower limit.

SKIPJACK TUNA HABITAT HYPOTHESIS

We hypothesize that skipjack tuna of the central and eastern Pacific Ocean occupy a primary habitat—a volume of water whose properties they can tolerate indefinitely—which is 18° C or warmer, but cooler than the upper limits for normally active animals shown in Figure 1b, provided that the dissolved oxygen concentration is at least 3.4 ml/l (5 ppm). Skipjack tuna can presumably

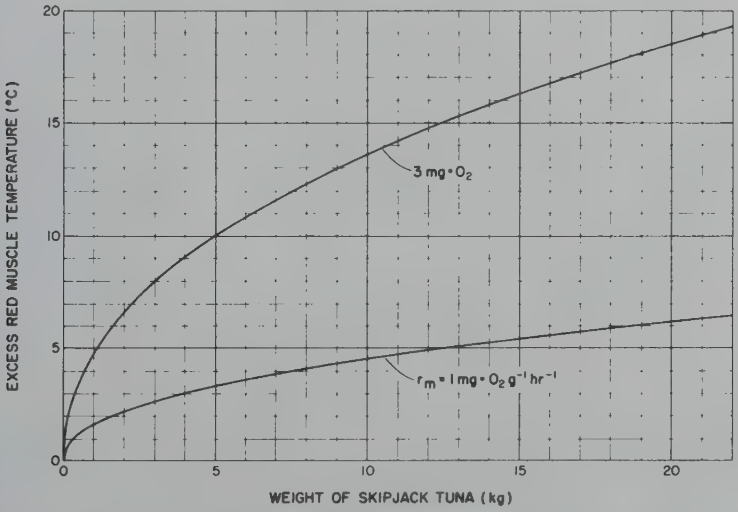

FIGURE 1a.—Calculated excess of internal temperature, over that of the surrounding water, in red muscle for skipjack tuna of all known sizes. Values are shown for a measured minimum (anesthetized) level of metabolic activity (lower line) and our estimate of the mean metabolic activity for normally active animals (upper line), triple the minimum level. (From Neill et al. 1976.)

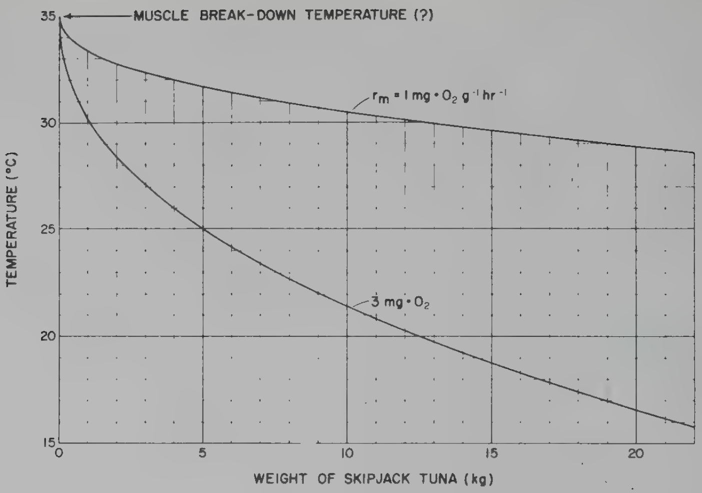

FIGURE 1b.—Maximum tolerable water temperature for skipjack tuna as a function of size for the same two rates of metabolic activity illustrated in Figure 1a. Based on calculated internal temperature excesses and the assumption that damage to red muscle tissue occurs above 35°C.

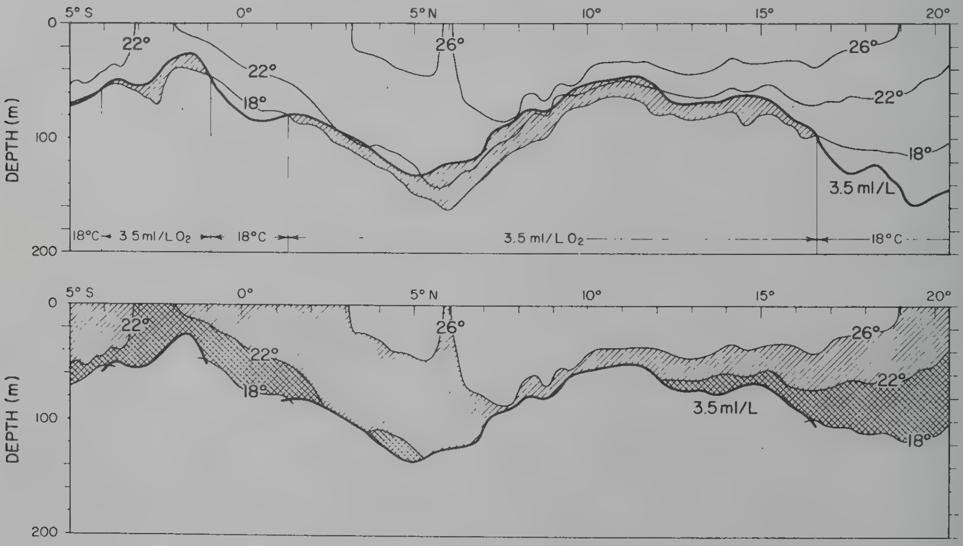

FIGURE 2.—Upper panel: Temperature and dissolved oxygen (selected isopleths only) along long. 119° W, eastern Pacific Ocean, August 1967 (Love 1972). Lower limits of the skipjack tuna habitat are assumed to be either 18° C or 3.5 ml/l dissolved oxygen, as indicated. The hatched layer should be warm enough for these fish, but oxygen deficient. Lower panel: Hypothesized habitat layers for skipjack tuna of two sizes, 4 kg (entire hatched area) and 9 kg (cross hatched area only) in the same section. Fish < 4 kg could presumably live anywhere between the sea surface and the lower limits, 18°C or 3.5 ml/l of dissolved oxygen.

leave their primary habitat only for limited periods of time without suffering thermal or oxygen stress. Prolonged excursions to colder water would require increased activity and thus more dissolved oxygen and food. Skipjack tuna could stay in the warm upper layers only if they would reduce their physical activity, or tolerate overheating. Hypothetical consequences of these conditions are illustrated in Figure 2 which shows the hypothetical layers along long. 119° W for skipjack tuna of two sizes. The 4-kg fish are those most abundant in catches by the eastern Pacific fishery; 9-kg fish are the largest normally found there, and then only in certain areas such as the Revillagigedo Islands (ca. lat. 17° N, long. 112° W).

The deeper limit of the habitat should be the same for skipjack tuna of all sizes. The upper limit is deeper and more restrictive for larger fish, which find essentially no habitable water between lat. 5° and 12° N, a distance of more than 700 km or 400 n.mi. Larger fish also have much less continuous access to the sea surface than those weighing 4 kg. Only skipjack tuna of the smallest size commonly found in this area (< 4 kg) could inhabit all of the water above the lower limits in Figure 2.

Figures 3 to 6 are maps of a hypothetical skipjack tuna habitat for the entire central and eastern Pacific Ocean, based on oceanographic station data used in preparing the Oceanographic Atlas of the Pacific Ocean (Barkley 1968). For these maps,

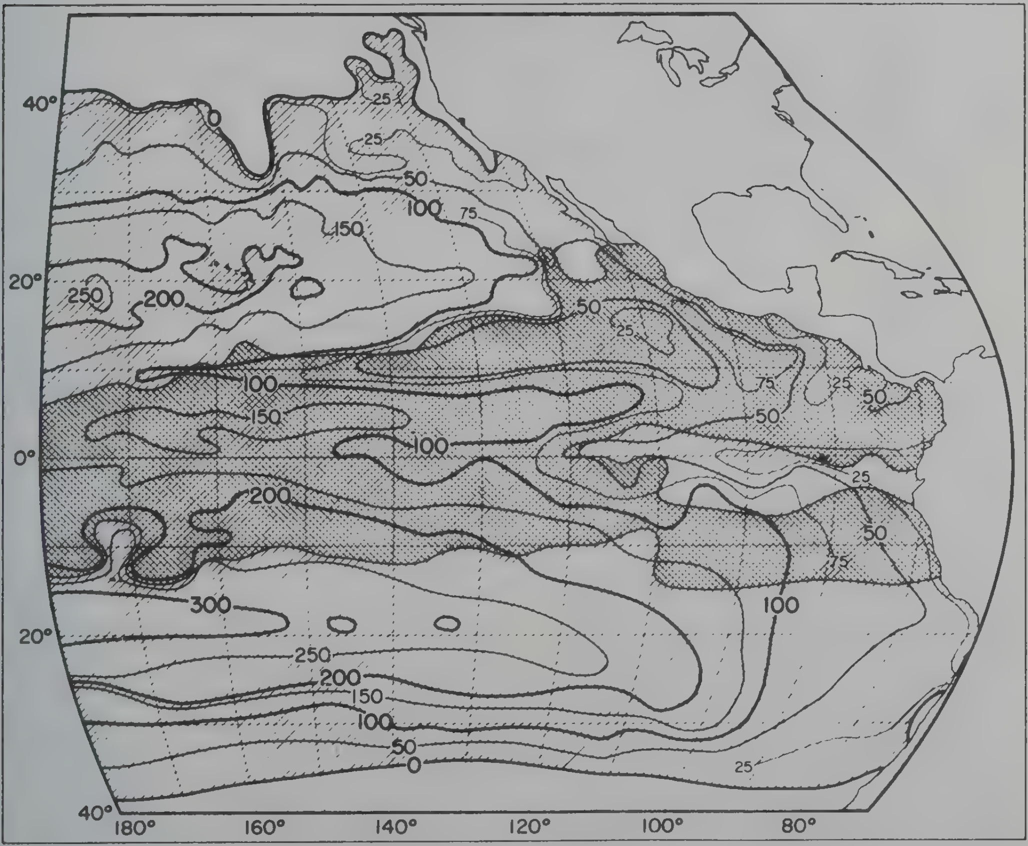

FIGURE 3.—Hypothetical maximum depth (meters) of the skipjack tuna habitat in the eastern Pacific Ocean, as determined by the depth of the 18°C isotherm (hatched area) or the 3.5 ml l (5 ppm) isopleth of dissolved oxygen (cross hatched area). Contour interval is 50 m except for a few areas near the coast, where a 25-m contour interval is used.

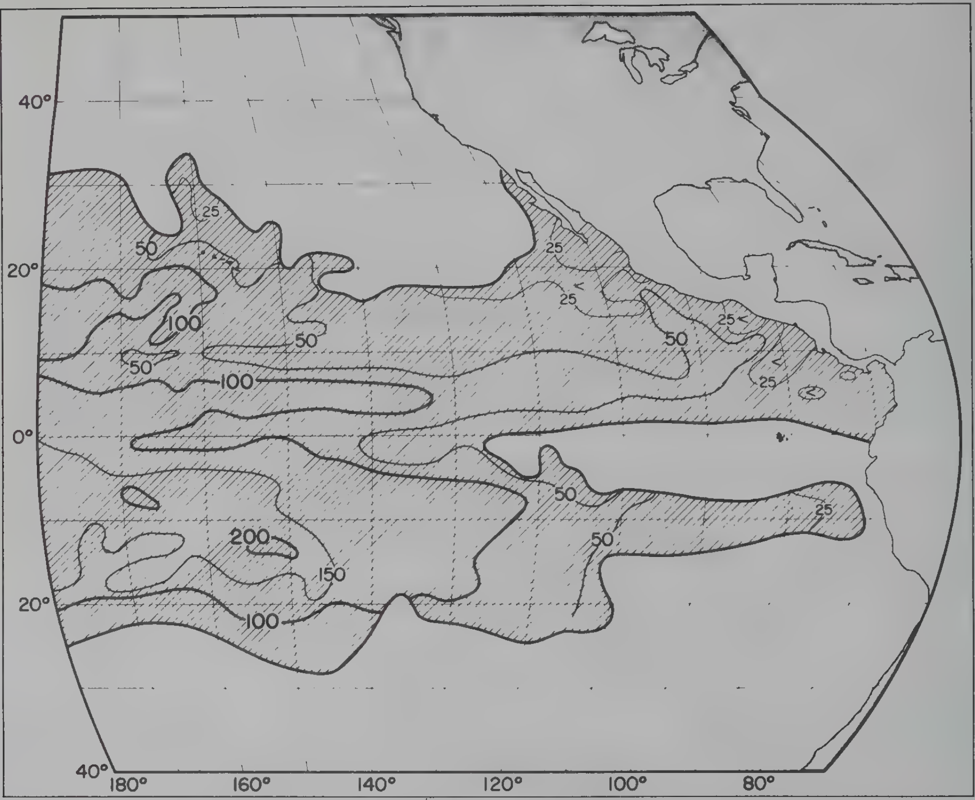

FIGURE 4.—Hypothetical minimum depth of the skipjack tuna habitat in the Pacific Ocean east of long. 180°, for fish weighing about 6.5 kg (14 lb) which are limited to water cooler than 24° C. Contours show the depth, in meters, of the 24° C isotherm.

station data were averaged within 2° areas of latitude and longitude, for all months, to approximate annual mean conditions.

Figure 3 shows the hypothetical "floor" of the skipjack tuna habitat, i.e., maximum depths (in meters) for this species. In Figure 3, the unhatched areas off the Pacific coast of the Americas, and at latitudes higher than about 40° in both hemispheres, indicate water which, at all depths, is colder on average than 18° C; presumably skipjack tuna would not normally be present.

Figure 4 shows the minimum habitat depth or ceiling for 6.5-kg fish. Outside of the hatched area annual mean surface temperatures are <24° C, and 6.5-kg fish would normally have access to all of the water column above the habitat floor (Figure 3), up to and including the sea surface.

Figure 5 shows the hypothesized habitat layer thickness for 6.5-kg skipjack tuna. In some areas, there is no water cooler than 24°C with more than 3.5 ml/l dissolved oxygen, so in these areas there is no habitat for 6.5-kg or larger fish; such areas are double hatched on Figure 5. Extensive regions around these areas have habitat layer thickness of 10 m or less, and large areas of the equatorial Pacific Ocean have <25 m of habitat layer thickness. This rather thin layer can lie beneath as much as 150 m of water warmer than 24° C (at lat. 4° N, long. 170° W, e.g.). North of the Hawaiian Islands, the opposite situation is present: a 150-m thick habitat layer lies under 25 to 50 m of water

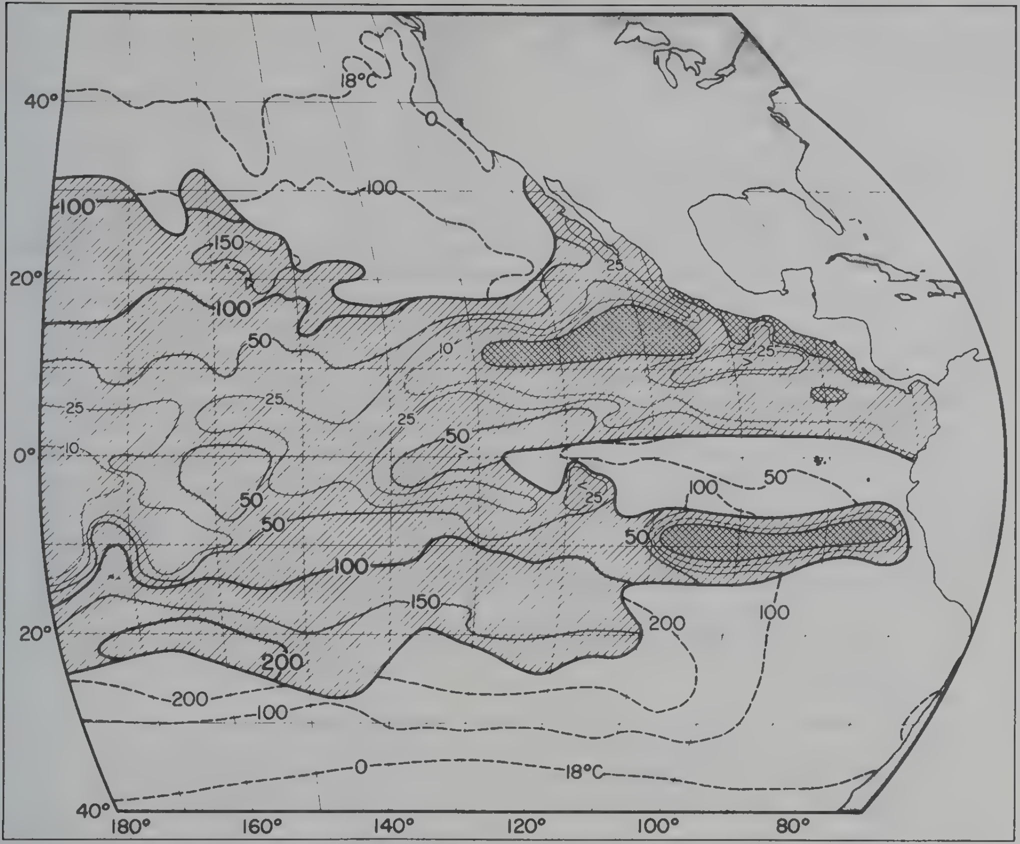

FIGURE 5.—Thickness of the hypothetical habitat layer (meters), for 6.5-kg skipjack tuna in the eastern and central Pacific Ocean. Contours were obtained by subtracting depths of the upper habitat limit (Figure 4) from the lower one (Figure 3). In the crosshatched areas off Mexico and Peru, there should be no habitat suitable for fish of this or larger sizes. In the hatched area, water warmer than 24°C is present above the habitat layer. Immediately beyond this area the habitat (dashed depth contours) extends to the sea surface. Outside of the 18°C surface isotherm, the water is probably too cold for skipjack tuna.

warmer than 24°C. Clearly, the South Pacific Ocean offers the roomiest habitat to large skipjack tuna, and in fact some of the largest known individuals of this species were caught slightly south of Tahiti (lat. 17°S, long. 150°W), according to catch records of longline fishing boats (R. A. Skillman, Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812, 1977, pers. commun.).

An interesting feature of the habitat map for 6.5-kg fish (Figure 5) is a channel of relatively cool and adequately oxygenated water some 200 km off the coast of Mexico. This channel should allow skipjack tuna as large as 6.5 kg to pass from the Baja California fishery to the equatorial fishery, or vice versa, when fish as small as 4 kg would find stressful conditions for hundreds of kilometers on either side of that channel. Seasonal and year-to-year closure or shifting of this channel could readily explain puzzling variations in the distribution of skipjack tuna catches in the eastern Pacific.

Figure 6 shows areas of presumably stressful environment (zero habitat thickness) in the eastern tropical Pacific for fish of various sizes and therefore temperature limitations. Skipjack tuna >11 kg should find no habitat at all within the shaded area. Fish 4 kg in size would find no habitat within the smallest contour (temperatures above

26° C). Fish weighing <4 kg should find some thickness of habitable water, within and just below the upper mixed layer, everywhere in the eastern tropical Pacific.

DISCUSSION

Although we anticipate that temperature and dissolved oxygen will prove to be primary determinants of the habitat of skipjack tuna in all oceans, it is possible that limiting values of these variables may differ from one population or region to another. The lowest temperature (ca. 15° C) at which skipjack tuna are caught in Australian waters (Robins 1952) is considerably lower than in the eastern Pacific. The fish caught off Australia may also differ in their ability to tolerate warm or low-oxygen water.

The gross features of the distribution of skipjack tuna in the eastern tropical Pacific, where only small skipjack tuna are found in large numbers (Williams 1970), agree with the hypothesis. Those areas where large skipjack tuna do occur (Matsumoto 1975) are outside of the hatched area in Figure 6; the Revillagigedo Islands, e.g., are just north of the hatched area, and Tahiti is well south of it.

The hypothetical habitat proposed here explains why skipjack tuna leave the northern fishery of the eastern Pacific when they reach a certain size. To find cooler, better oxygenated water as they grow, these fish must move out of the eastern tropical Pacific toward higher latitudes in the central Pacific. Also, they must then spend less time at or near the sea surface, since the thermocline, where they live, is generally much deeper in the central Pacific, and the water above the thermocline is too warm to permit normal activity. This size-specific movement in response to the environment is consonant with Rothschild's (1965) migration model for the eastern Pacific skipjack tuna population. It also suggests a mechanism for the evolution of migratory processes, an important topic in marine ecology.

For several reasons, existing fishery data are inadequate for making a refined judgment of our skipjack tuna-habitat hypothesis: 1) Commercial fishery data generally include neither information

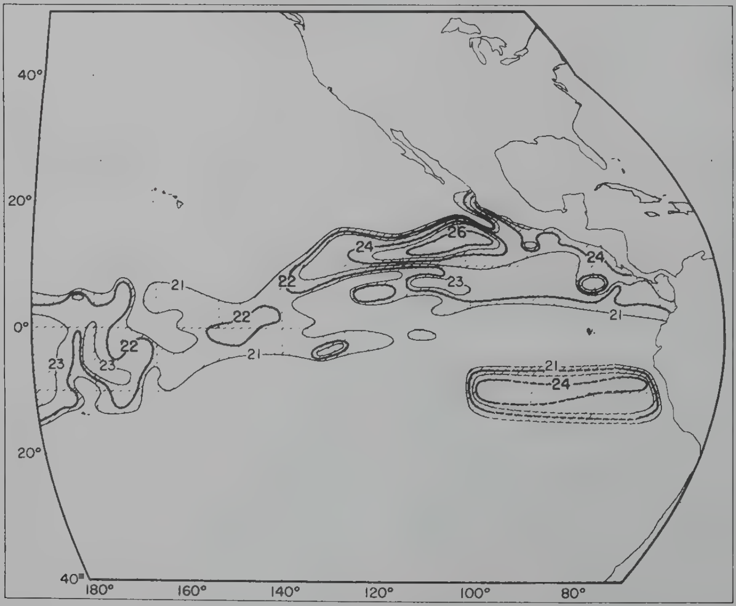

FIGURE 6.—Average water temperature in the eastern Pacific Ocean at those depths where the concentration of dissolved oxygen is 3.5 ml/l. Deeper water is cooler and lower in oxygen, shallower water is warmer and has more oxygen. See Figure 1b for the relationship between skipjack tuna size and upper temperature limits.

on individual sizes of skipjack tuna composing the catch nor synoptic information on the vertical distribution of temperature and dissolved oxygen in the fishing area. 2) The degree to which catch per unit effort measures fish abundance may vary greatly with gear type, fish size, and environmental conditions. For example, the habitat hypothesis implies that purse seines (which fish the upper 50 m or so of the water column) should be most effective in those parts of skipjack tuna habitat with a shallow floor. In fact, the eastern Pacific purse seine fishery operates almost entirely in waters with a skipjack tuna habitat-floor at depths of 50 m or less (c.f. our Figure 3 and fig. 1 of Matsumoto 1975). Efforts to catch skipjack tuna by purse seining in Hawaiian waters—where the habitat-floor lies at depths near 200 m (Figure 3)—have been ineffectual (Murphy and Niska 1953). Green (1967) reported strong positive correlations between the success of purse seining for eastern Pacific skipjack tuna and yellowfin tuna, *Thunnus albacares*, and the presence of shallow (≤60 m to top), steep (≥0.55°C cm⁻¹) thermoclines. 3) Commercial fishermen naturally fish only where they expect to find and catch fish; thus, fishing effort tends to be very unevenly distributed.

A partial test of the habitat hypothesis might be achieved through experimental fishing in and near the hatched areas of Figure 6; fishing effort, the sizes of captured skipjack tuna, and vertical distributions of temperature and dissolved oxygen would need to be measured at each fishing location. But, experimental fishing—even if conducted in a thorough and systematic fashion—might not yield a conclusive test of the hypothesis, because there would still be no guarantee that catch per unit effort accurately reflected fish abundance (reason 2 above).

We advocate, instead, the application of ultrasonic telemetry to test the skipjack tuna-habitat hypothesis. Because skipjack tuna tagged with ultrasonic transmitters tend to stay with their school (Yuen 1966) and because skipjack tuna schools tend to be homogeneous with respect to fish size (Brock 1954), the track of a single tagged fish could be taken as representative of a large number of normally behaving, similarly sized fish. Pressure-sensitive ultrasonic transmitters (like that described by Luke et al. 1973) would permit continuous monitoring of fish position in all three spatial dimensions through time. Spatial-temporal coordinates of fish could then be compared with synoptic data on vertical distributions of temperature and dissolved oxygen. A few dozens of such comparisons, for fish of various sizes in waters with diverse vertical distributions of temperature and dissolved oxygen, would constitute a valid and sufficient test of the habitat hypothesis. Toward this end, preliminary telemetry work is now underway at this Laboratory.

SUMMARY

Work with captive skipjack tuna at this Laboratory has yielded information on the temperature and dissolved oxygen requirements of this species. If these laboratory results apply to skipjack tuna in nature, they provide new insight into the evolution of migration in skipjack tuna populations, make it possible to account for the geographic distribution of skipjack tuna on the basis of environmental conditions, and provide means for predicting their movements in major fisheries such as those of the eastern tropical Pacific.

In particular, we suggest that only young skipjack tuna can inhabit tropical surface waters, and that the habitat of adult skipjack tuna in the tropics is the thermocline and not the warmer surface layer, as has generally been thought. Since the thermocline in many areas is too oxygen-poor to support these active fish and the well-oxygenated surface layer is too warm for adult skipjack tuna, only heat-tolerant young skipjack tuna can live in those areas. As they grow, these fish are forced to move into areas where well-oxygenated water of the proper temperature is more readily available.

Up to now, it has not been possible to trace the movements of migrating skipjack tuna largely because they move through areas of many millions of square miles, at unknown depths. Knowledge of their temperature and dissolved oxygen requirements dramatically reduces the scope of the problem: the fish should be in a well-defined layer of water, of directly and easily measured thickness, whose geographic extent can be sharply defined with either historical or current oceanographic observations.

ACKNOWLEDGMENTS

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SECTION 18

HISTORY OF CHANGES IN FISH SPECIES OF THE GREAT LAKES

John F. Carr

INTRODUCTION

Changes began in the fish-species complex in the Laurentian Great Lakes almost immediately after the first permanent settlers arrived in the basin in the early 1800's. Changes occurred slowly at first, but accelerated with the increased activities of man. These changes continue today and will continue in all probability for decades or even centuries because man's manipulations of the environment are continuing.

The Great Lakes are young; only about 10,000 years have passed since the melting of the glaciers. Youthful lakes such as these are generally characterized by low biological productivity, low nutrient content, and high transparency; they are often deep and cold. So are the Laurentian Great Lakes even today. With the exception of a few areas, the waters of the Great Lakes are of excellent quality and can be used as potable water without treatment. Yet man's impact on these lakes, especially on the fish populations, has been so drastic that the Laurentian Great Lakes have been used as worldwide symbols of accelerated aging. Some scientists have estimated that the lakes, especially Erie and Ontario, have aged more in the past 150 years than in the preceding 10,000 years. That changes of this magnitude could occur in lakes as large as the Great Lakes was not considered possible only a few years ago. Today, however, we are beginning to realize the tremendous capacity we possess to change (usually to our detriment) even the oceans and the atmosphere.

The purpose of this paper is to discuss the changes which have taken place in the fish populations of the Great Lakes and the stresses which have caused these changes. It has become obvious that many of the causes of the declines are the results of deliberate actions rather than subtle unpredictable factors.

The stresses which have been placed on the fish communities of the Great Lakes have been sequential and reflect the progress of man's occupation of the basin and his technological development. The most obvious and primary direct stress has been the intensive and selective exploitation of the fish stocks. This stress began early in the 19th century and continues to some degree today. Environmental stresses have not been as direct or as obvious, but were present as early as 1830 and have been additive as well as continuous. Environmental stress on the fish of the Great Lakes has been of five general types:

(1) Physical stress resulting from modification of the watershed by deforestation, blockage of tributaries, and drainage of marshes. This primarily affected anadromous species and began during the period of low human population density.

(2) Biological stress caused by the introduction and colonization of exotic species. Introduction of new species began before 1900 and continues today.

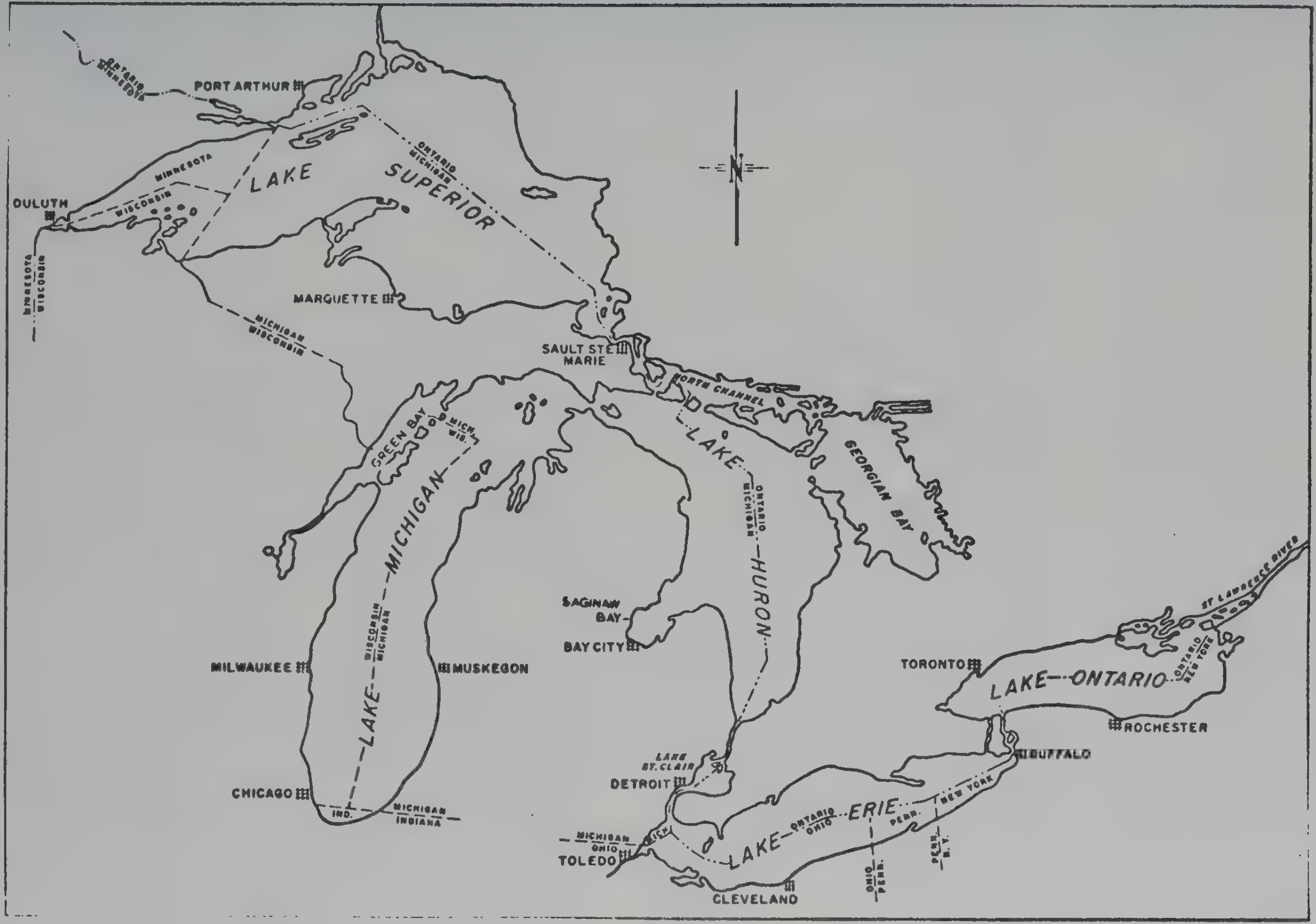
(3) Chemical stress (first phase) in the form of oxygen-consuming organic material dumped into tributaries and bays, and increased plant nutrients in the inshore areas.

(4) Chemical stress (second phase) caused by toxic chemicals such as chlorinated hydrocarbons and heavy metals.

(5) Thermal stress - more a future concern than a present concern.

The direct effects of the environmental changes on the fish populations are seldom observed and perhaps rarely occur. Indirect effects of these changes are often cited, but only occasionally quantified. In lakes as large as the Great Lakes, cause and effect are separated in time and distance to an extent that only after an event can the two be linked. This is the situation with the continuous change in the abundance of Great Lakes fish species.

We all recognize the fact that the stresses, be they exploitation, destruction of spawning grounds, oxygen depletion, increased water temperature, change in available food, or competition with introduced species, cannot often be isolated and analyzed separately. This paper is a summary of the changes that have occurred in the fish communities of the Laurentian Great Lakes from the early 19th century to the present. The changing composition of fish populations in the Great Lakes has been the subject in recent years of many articles in scientific and popular publications. The most exhaustive discussion of these changes occurred in a recent (1971) international symposium on "Salmonid Communities in Oligotrophic Lakes" (SCOL). These papers were published as a special issue of the Journal of Fisheries Research Board of Canada in 1972. This publication contains seven papers exclusively on the Great Lakes, including case histories of each of the five Laurentian Great Lakes: Superior, Huron, Michigan, Erie, and Ontario (Figure 1). Other comprehensive papers on changes in Great Lakes fish species are by Smith (1964, 1968) and Christie (1974).


PORT ARTHUR
ONTARIO
MINNESOTA
LAKE
SUPERIOR
ONTARIO
MICHIGAN
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WISCONSIN
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MARQUETTE
MICHIGAN
WISCONSIN
SAULT STE MARIE
NORTH CHANNEL
GREEN BAY
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MICHIGAN
LAKE
HURON
ONTARIO
MICHIGAN
GEORGIAN BAY
SAGINAW BAY
BAY CITY
MILWAUKEE
MUSKEGON
CHICAGO
IND.
MICHIGAN
INDIANA
LAKE ST. CLAIR
DETROIT
MICHIGAN
OHIO
TOLEDO
MICH.
LAKE
ERIE
ONTARIO
OHIO
PENN.
NEW YORK
OHIO
PENN.
PENN.
N.Y.
CLEVELAND
BUFFALO
TORONTO
LAKE
ONTARIO
ONTARIO
NEW YORK
ROCHESTER
ST LAWRENCE RIVER
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Figure 1. The St. Lawrence Great Lakes with interstate and international boundaries.

IN THE BEGINNING (TO 1850)

Fish Communities

The fish-species complex in the Great Lakes has changed drastically. Unlike many large lakes of the world, especially the large African lakes and Lake Baikal (USSR), the Laurentian Great Lakes have had only 10 thousand years between the retreat of the glaciers and the coming of man to produce, through evolutionary forces, a complex of species that is unique to the system.

The Great Lakes system did produce a few unique species in this short period, indicating that the processes were well underway to further species diversity. The evidence for this conclusion is best illustrated by the five endemic species (Smith, 1957; Scott and Crossman, 1973), all of the subfamily Coregoninae (whitefish) in the Samonidae (salmon family). These five species listed in descending order of size were:

deepwater cisco - *Coregonus johannae*
longjaw cisco - *Coregonus alpenae*
shortnose cisco - *Coregonus reighardi*
kiyi - *Coregonus kiyi*
bloater - *Coregonus hoyi*

According to Scott and Crossman (1973) all five species were found in Lakes Huron and Michigan, four in Lake Superior, three in Lake Ontario, and one in Lake Erie.

In addition to the five endemic species of ciscos, these wider ranging species were also present: lake herring (*Coregonus artedii*); blackfin cisco (*Coregonus nigripinnus*); and shortjaw cisco (*Coregonus zenithicus*). These eight species of ciscos, together with the lake whitefish (*Coregonus clupeaformis*) and round whitefish (*Coregonus cylindraceum*), characterized the Great Lakes fish community. Most of the species of the whitefish subfamily, especially the ciscos, were inhabitants of deep, cold water and therefore reached their greatest diversity in Lakes Superior, Huron, Michigan, and Ontario (Table 1). The dramatic alteration in the species complex of deepwater ciscos that subsequently occurred was documented by Smith (1964) for Lake Michigan.

In addition to the Coregonines other groups and species were abundant in the lakes. The dominant predators of the open waters present in all five lakes were the lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*). In the bays and nearshore areas were: lake sturgeon (*Acipenser fulvescens*); northern pike (*Esox lucius*); suckers (primarily *Catastomus catastomus* and *C. commersoni*); channel catfish (*Ictalurus punctatus*); bullheads (*Ictalurus* spp.); white bass *Morone chrysops*; freshwater drum (*Aplodinotus grunniens*); and three species of the perch family: yellow perch (*Perca flavescens*); walleye (*Stizostedion vitreum*); and sauger (*Stizostedion canadense*). All of these species have been historically of commercial significance. The Atlanta salmon (*Salmo salar*) and American eel (*Anguilla rostrata*) were also abundant and became commercially important only in Lake Ontario.

TABLE 1. DIMENSIONS OF THE GREAT LAKES[a]

Lake	Length (miles)	Breadth (miles)	Water surface (miles)	Drainage basin (miles)	Average surface elevation above mean sea level since 1860 (ft)	Mean discharge (cfs)	Maximum depth (ft)	Mean depth (ft)
Superior	350	160	31,820	80,000	602.20	73,300	1,333	487
Michigan	307	118	22,400	67,860	580.54	55,000	923	276
Huron	206	183	23,010	72,620	580.54	177,900	750	195
St. Clair	26	24	490	7,430	574.88	178,000	21	10
Erie	241	57	9,930	32,490	572.34	195,800	210	58
Ontario	193	53	7,520	34,800	246.03	233,900	802	283

[a] From Beeton and Chandler, 1963.

Knowledge of the presence and relative abundance of the species listed thus far is based on records of the harvest of these species by commercial fishermen. Species not of great commercial value were, of course, also present in the lakes. A complete list of all species known to have been present in the lakes would be too long to include for the purposes of this paper. Our knowledge of changes in abundance of a few of these species, however, is sufficient to warrent their inclusion. An abundant forage species in the deeper water of all the lakes was the fourhorn sculpin (Myoxocephalus quadricornis). The slimy sculpin (Cottus cognatus) inhabited intermediate depths in all lakes. The inshore waters contained a variety of species of several families, especially the Cyprinidae. Among the more abundant species were the emerald shiner (Notropis atherinoides) and the spottail shiner (Notropis hudsonius).

Thus, when settlement began in the first half of the 19th century, the lakes were occupied by a supposedly stable community of fish species which inhabited all niches from the deepest waters of the subartic Lake Superior to the shallow bays and marshes of Lake Erie.

Environmental Conditions

Physiochemical conditions of the lakes were not measured before the end of the 19th century. Beeton and Edmondson (1972) used as a basis for evaluating the "natural" chemical condition the limited chemical data available about 1900 as indicative of the pristine quality of the lakes (Table 2).

TABLE 2. ESTIMATED AVERAGE CONCENTRATION OF DISSOLVED CHEMICAL CONSTITUENTS IN THE GREAT LAKES PRIOR TO 1900 (EXPRESSED IN MG/LITER)[a]

Lake	Total dissolved solids	Calcium	Sulphate	Chloride	Sodium and potassium
Superior	60	13	4	2	3
Michigan	128	34	5	2	-
Huron	108	24	6	4	4
Erie	142	31	13	7	7
Ontario	140	31	15	7	6

[a] From Beeton, 1969.

Based on these few constituents, Lakes Michigan, Erie, and Ontario were similar in chemical composition (Table 2). Lake Superior's chemical levels were substantially below all the others. Lake Huron receives approximately 41% of its inflow from Lake Superior, 31% from Lake Michigan, and 28% from the Lake Huron basin. Apparently the basin is a major contributor to the characteristics of the water quality, because the total dissolved solids are much higher than would be expected based only on a mixture of the waters from Lakes Superior and Michigan. The Lake Erie watershed apparently contributed significant amounts of calcium, sulphate, chlorides, and sodium-potassium to the waters flowing into Lake Ontario, because their chemical characteristics are nearly identical. Although differences between lakes were large compared to the range between other natural bodies of water, the five Great Lakes were remarkably similar.

Analysis of nutrient concentrations for the Great Lakes has been made only in recent years; therefore, base levels are only now being established. Estimates based on recent values for phosphorus and nitrogen indicate that the levels in the mid-1800's were less than 10 μg/liter for phosphorus and usually less than 1 mg/liter for total nitrogen in the three upper lakes (Superior, Huron, and Michigan). The Great Lakes in the 1900's would have been classified as oligotrophic (as defined by Hutchinson, 1957) with the probable exception of Lake Erie.

The order of the lakes, if listed from the greatest to the least fishery productive potential in the 1800's, probably would be Lake Erie, Lake Ontario, Lake Michigan, Lake Huron, and Lake Superior (Figure 2).

THE INITIAL IMPACT OF SETTLEMENT (1850-1900)

Changes in Fish Populations

The first environmental stresses on the Great Lakes ecosystem were primarily caused by physical alterations in the basin, particularly in the lower lakes. These alterations were deforestation of the watershed and siltation and blockage of streams. These changes mainly affected the tributaries and consequently the obligate anadromous species. Christie (1972) reported the Atlantic salmon had begun to decline as early as 1830 in Lake Ontario and was extinct, or nearly so, by 1900. Documentation of the early proliferation of mills and dams was given by Christie (1972) based on data from Richardson (1944). On the Ganaraska watershed (one of the larger Canadian rivers tributary to Lake Ontario) at least two sawmills, two grist mills, and two dams had been constructed by 1800. Construction of the mills and dams increased rapidly, reaching a maximum of 34 sawmills, 19 grist mills, 4 woolen mills, and 34 dams by 1860. In 1930, 15 dams still remained on this single tributary. Christie (1972) considered the elimination of the Lake Ontario Atlantic salmon stock as the best known example of the effects of despoilation on a species habitat.

The lake sturgeon population in all the lakes was greatly reduced during this period. Prior to 1903 the annual commercial production fluctuated between 100,000 pounds and 500,000 pounds in Lake Ontario (Baldwin and

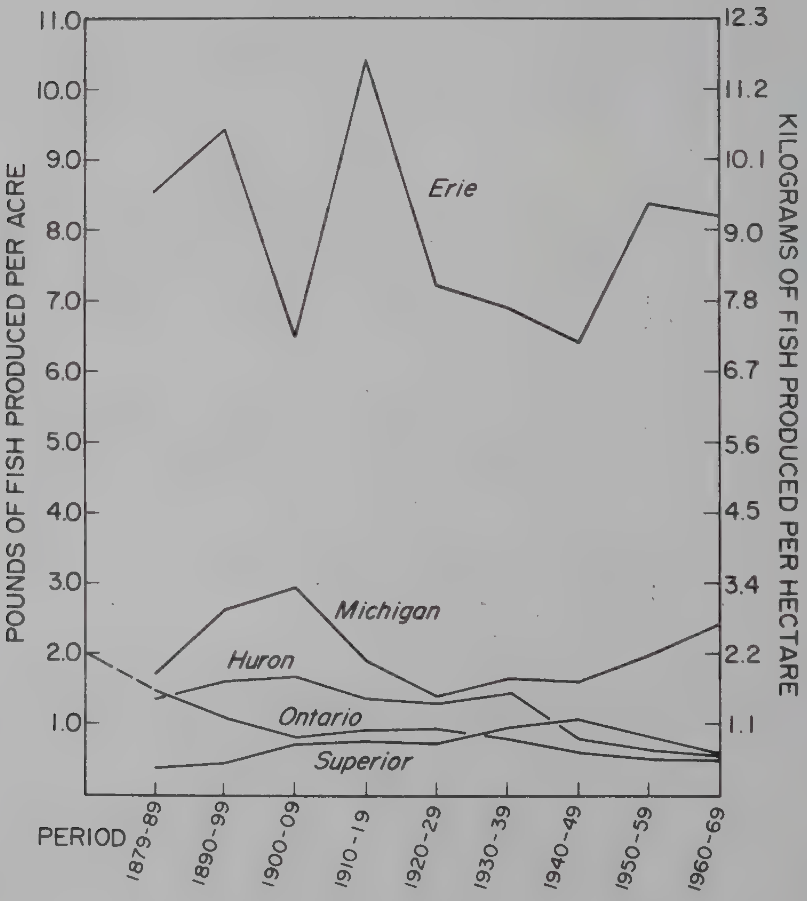

Figure 2. Average number of pounds and kilograms of fish produced per acre and hectare by the commercial fishery of the Great Lakes for 10-year intervals (data from Smith 1972).

Saalfeld, 1962). After 1910 production never exceeded 25,000 pounds and averaged near 15,000 pounds for many years. In Lake Erie production dropped from 1 - 5 million pounds in the late 1800's to less than 10,000 pounds after 1910 (Baldwin and Saalfeld, 1962). Similar magnitudes of decline occurred during the same period in Lake Huron, Michigan, and Superior. The cause-and-effect relationship apparent between watershed and stream modification and Atlantic salmon extinction was not as direct with the sturgeon. The environmental requirements of the sturgeon were not as narrow as those of the Atlantic salmon; however, the slow growth rate and late maturity of the sturgeon were also factors in this species, inability to recover from even low exploitation rates.

Christie (1972) also lists the blackfin cisco (Coregonus nigripinnus) as a species that became either extinct or greatly reduced in Lake Ontario before 1900. Wells and McLain (1972) infer a sharp decline in the abundance of this species in Lake Michigan in the early 1900's. The blackfin was considered commercially extinct in Lake Superior by 1910 (Lawrie and Rahrer, 1972). This species of cisco inhabited the deep, open waters of the lakes; consequently, environmental modification of the tributary and watershed was not a factor in their decline. This species was the largest of the ciscos, and selective exploitation for it was the probable cause of its decline (Wells and McLain, 1972).

The lake trout population in Lake Erie was also decimated during this period. Hartman (1972), in discussing this species in Lake Erie, states: "Perhaps the decline of the lake trout population to near extinction best illustrates the effect of essentially one stress: intensive exploitation." Apparently, environmental stress was not a factor in the decline of lake-dwelling species during the 1800's.

In addition to the effective loss of at least one species during the 1800's, several new species became abundant. Christie (1972) listed the following species as becoming established in Lake Ontario before 1900: alewife (Alosa pseudoharengus); gizzard shad (Dorosoma cepedianum); brown trout (Salmo trutta); carp (Cyprinus carpio); and the goldfish (Carassius auratus). Some of these species were also introduced to the other lakes during this period. There was a flourishing fishery for carp in Lake Erie by 1899, when over 3.5 million pounds were landed (Baldwin and Saalfeld, 1962).

Environmental Changes (Age of Physical Alterations)

Man's effect on the Great Lakes ecosystem in the last half of the 19th century was dramatic and permanent. He removed the forest, built dams, constructed mills, directly exploited the fish, and opened new and more direct passage between the ocean and the lakes, as well as between Lake Ontario and the upper lakes (Figure 3).

The effects of these physical modifications of the environment ranged from immediate (Atlantic salmon extinction) to long-term (invasion of marine species). The Erie Canal, which provided a connection between the Atlantic Ocean and Lake Ontario, was opened in 1819 and extended to Lake Erie in

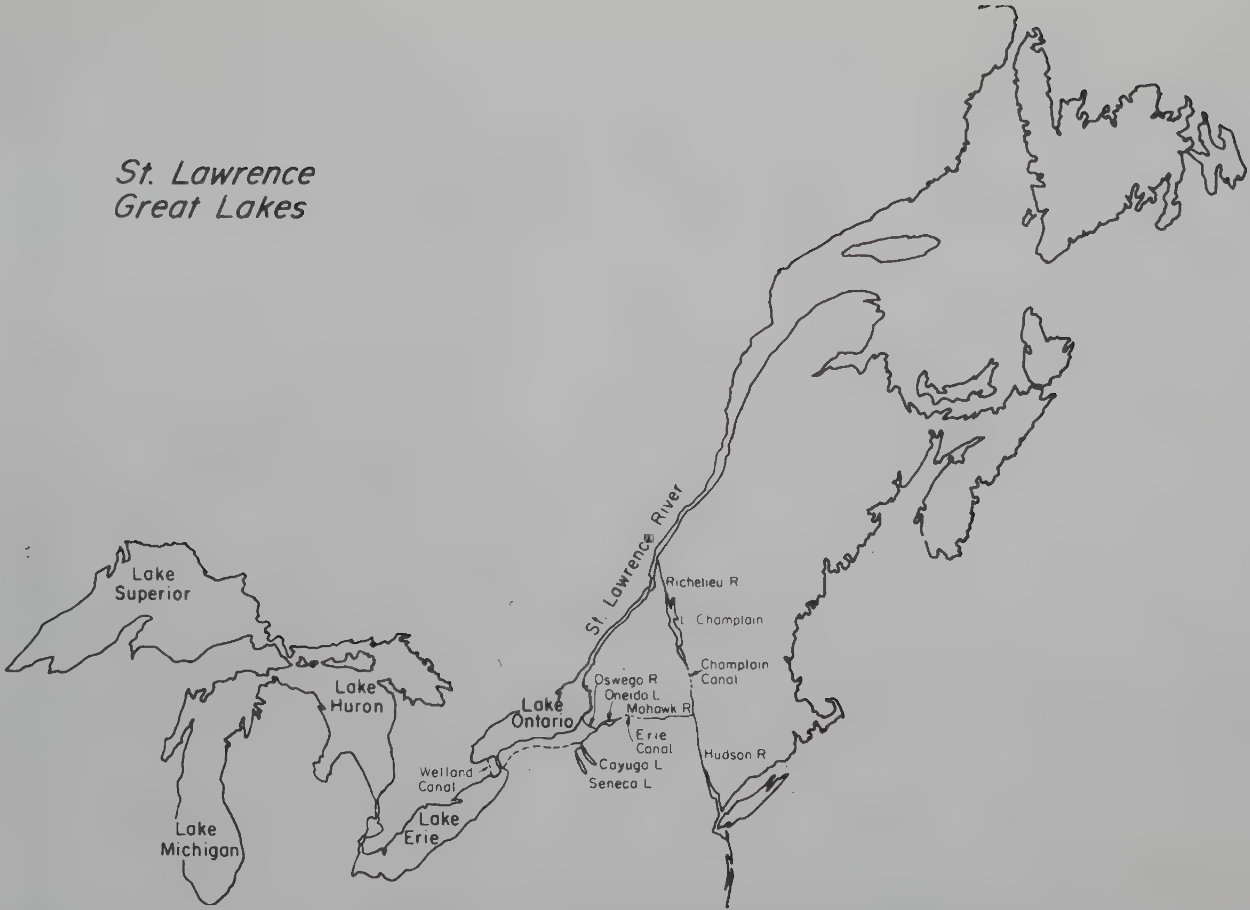
St. Lawrence
Great Lakes
Lake Superior
Lake Michigan
Lake Huron
Lake Erie
Welland Canal
Lake Ontario
St. Lawrence River
Oswego R
Oneida L
Mohawk R
Erie Canal
Cayuga L
Seneca L
Richelieu R
L Champlain
Champlain Canal
Hudson R

Figure 3. The St. Lawrence Great Lakes showing canals between central Atlantic Ocean and the lakes.

1825. The Welland Canal, which was opened in 1829, connected Lake Ontario to the upper lakes. Previously the passage of fish between Lakes Ontario and Erie was blocked by Niagara Falls. Although no biological changes were noticed for many years after the opening of the canals, the stage was set for dramatic and catastrophic changes to occur decades later (Aron and Smith, 1971).

The chemical characteristics of the open waters of the lakes were assumed to be essentially the same at the end of the 19th century as at the beginning (Beeton and Edmondson, 1972). Although the settlement of the Great Lakes basin had advanced rapidly in the 19th century, from a population of a few thousand early in the century to over 10 million in 1900 (Table 3), the effects on water quality in the lakes were yet to be felt.

By 1900 man, in less than 100 years, had placed the following stresses on the biological communities of the Great Lakes: siltation of streams; blockage of tributaries; increase in stream temperatures; and establishment of exotic species. In addition, he had removed barriers to migration between the lakes; had established fisheries capable of overexploitation of most species in all the lakes; and had begun using the lakes as the receiver of man's domestic and industrial waste.

TABLE 3. ESTIMATED POPULATION (MILLIONS) IN GREAT LAKES BASIN - 1900-1960[a]

Lake basin	1900	1925	1950	1960
Superior	0.4 (50)[b]	0.6 (33)	0.8 (12)	0.9
Michigan	4.0 (-20)	3.2 (50)	4.8 (23)	5.9
Huron	1.0 (20)	1.2 (25)	1.5 (33)	2.0
Erie	3.0 (93)	5.8 (48)	8.6 (17)	10.1
Ontario	2.0 (25)	2.5 (20)	3.0 (33)	4.0
Total	10.4 (28)	13.3 (41)	18.7 (22)	22.9

[a] From Beeton, 1969.

[b] Numbers in parentheses indicate percentage change in the ensuing time interval.

ENRICHMENT AND INVASION (1900-1950)

The stage was set and the signs were present in 1900 for what was to follow. Changes in the biological, chemical, and physical environment of the Great Lakes became the rule and not the exception. The records of these changes, unfortunately, are incomplete, often inaccurate, and, for the fish populations, often not a true representation of species abundance. The analysis of changes in the abundance of species until recently was based on the reported catch of commercial fishermen. High prices often maintained high catches in the face of a decreasing abundance. Conversely, low production often was due to low prices and lack of demand for a species rather than low population levels. Despite these handicaps, the changing conditions often became too obvious to be ignored.

Changes in fish-species composition, losses and gains, differ in time between the lakes, but the sequence of species change often was similar (Smith, unpublished manuscript). In general, the species that declined were those most sought after by the commercial fishery. A few significant exceptions exist to this generalization, and it is the exceptions which clearly indicate stresses other than fishing on the biological communities of the Great Lakes.

Changes which occurred in native fish species of commercial interest between 1900 and 1971 are summarized in Table 4. Detailed discussion of these declines by species and lakes appear in Smith (1968), the papers of the SCOL Symposium (1972), and Christie (1974). The data presented in Table 4 refer to production trends in the total lake and, therefore, are not descriptive of events in the unique ecological areas of each lake such as the Bay of Quinte in Lake Ontario, the western basin of Lake Erie, Saginaw Bay of Lake Huron, or Green Bay of Lake Michigan (Figure 1). These geographic areas were, and are, more shallow and productive and warmer than the open portions of the lake to which they are connected. The fish-species complex here was also more diverse than in the open lake, containing many warmwater species, especially the centrarchids and percids.

Ecological and Cultural Changes, 1900-1925

During the first quarter of the 20th century, the northern pike fishery was reduced to a fraction of former production; lake whitefish in Lake Ontario and lake herring in Lake Erie began declining; the first sea lamprey was reported in Lake Erie; and the first rainbow smelt were found in Lakes Michigan and Huron. The gains and losses in these and other species were to be repeated many times in the next 50 years in the other lakes.

The introduction of the smelt into Crystal Lake in the drainage basin of Lake Michigan was deliberate, but its establishment in Lake Michigan was not contemplated, nor was its rapid spread to other Great Lakes. The sea lamprey reached Lake Erie nearly 100 years after the Welland Canal was opened and established itself in the upper lakes. The beginning of the declines in lake whitefish and lake herring were, of course, undetected at the time and thus alarmed no one.

TABLE 4. SUMMARY OF FISH SPECIES DECLINE IN THE GREAT LAKES BY YEAR, LAKE, AND CURRENT COMMERCIAL PRODUCTION

Species and lake	Beginning of decline (year)	Product first below 100,000 pounds (year)	1974 production (1,000's pounds)	Potential for recovery (H,M,L)[a] and reason
Lake trout				
Ontario	1928	1942	1	H - stocking and sea lamprey control (s.l.c.)
Erie	?	1900	0	L - environmental
Huron[b]	1935	1945	1	H - stocking & s.l.c.
Michigan	1943	1950	37	H - stocking & s.l.c.
Superior	1950	c	526	H - stocking & s.l.c.
Lake whitefish				
Ontario	1924	1966	16	L - environmental
Erie	1953	1960	1	L - environmental
Cisco (chubs)				
Ontario	1941	1950	0	L - environmental
Huron[b]	1961	1970	50	L - environmental
Michigan	1970	c	3,267	L - environmental
Superior	1965	c	1,926	L - environmental
Lake herring				
Ontario	1941	1953	32	L - environmental
Erie	1924	1958	0	L - environmental
Huron[b]	1939	1957	2	L - environmental
Michigan	1952	1963	6	L - environmental
Superior	1961	c	2,186	M - stocking
Northern pike				
Ontario	1933	1938	21	L - environmental
Erie	1914	1924	15	L - environmental
Burbot				
Ontario	1930[d]	1934[e]	0	L - environmental
Erie	1947	1961[e]	0	L - environmental
Michigan	1948[d]	1959	230[f]	H - s.l.c.
Blue pike				
Ontario	1952	1955	0	L - environmental
Erie	1955	1959	0	L - environmental
Sauger				
Erie	1945	1955	0	M - stocking
Huron	1935	1937[e]	0	L - environmental

[a] H, M, and L indicate high, medium, and low potential for recovery, respectively.

[b] Excludes Georgian Bay and North Channel.

[c] Remains above 100,000 pounds.

[d] Production normally less than 100,000 pounds.

[e] Production less than 10,000 pounds.

[f] First exceeded 100,000 pounds in 1973.

Environmental changes, except in streams and bays near centers of high human population density, were nearly undetectable in 1925 in the lakes proper. Changes had occurred, however, in Lakes Michigan, Erie, and Ontario in the few chemical constituents for which data are available (Table 5). The absolute concentrations of these constituents, even the highest levels, were well below levels of ecological or toxicological concern. The rates of change, especially in total dissolved solids, sulphur, and chloride, however, are staggering considering the tremendous volume of water which had been changed as much as 160% in only 25 years.

TABLE 5. ESTIMATED AVERAGE CONCENTRATION OF DISSOLVED CHEMICAL CONSTITUENTS IN THE GREAT LAKES IN 1925 (EXPRESSED IN MG/LITER)[a] WITH PERCENTAGE CHANGE AFTER 1900 IN PARENTHESES

Lake	Total dissolved solids	Calcium	Sulphate	Chloride	Sodium and potassium
Superior	58 (-3)	13 (0)	4 (0)	2 (0)	3 (0)
Michigan	143 (+12)	34 (0)	13 (+160)	4 (+100)	-
Huron	108 (0)	24 (0)	9 (+50)	4 (0)	4 (0)
Erie	146 (+3)	33 (+6)	16 (+23)	11 (57)	7 (0)
Ontario	149 (+6)	34 (+10)	18 (+20)	11 (57)	7 (17)

[a] From Beeton, 1969.

The increase in population growth in the basins of the Great Lakes was approximately 28% between 1900 and 1925 (Table 3). Growth in numbers was greatest in the basins of Lakes Erie and Ontario. The population in the Erie basin increased 93% to 5.8 million, and in the Lake Ontario basin the increase was 25% to 2.5 million. Lake Michigan's basin effectively lost 0.8 million when the Chicago Sanitary Canal, which diverted the waste from the city to the Mississippi River drainage, was completed in 1900. The increasing urbanization and industrial expansion was the probable cause of the increase in the chemically conservative ions. Undoubtedly, concentrations of other chemical components also increased, especially the plant nutrients phosphorus and nitrogen. The load of oxygen-demanding organic compounds can also be assumed to have increased.

The stresses causing the decreases in some native fish species in the lower lakes by 1925 were man caused, principally by heavy exploitation. The role of environmental change, especially water-chemistry change, in reduction in fish populations apparently was minor except in the tributaries and bays. The drainage of marshes, however, may have been a significant factor in the loss of the northern pike as an important commercial species in Lake Erie. The establishment of the two marine species, smelt and lamprey, was too recent to have had a measurable impact on other fish species by 1925.

Environmental and Cultural Changes, 1925-1950

Several catastrophic events affecting the Great Lakes fish stocks occurred during this period. The most damaging event was the invasion by the parasitic sea lamprey of all the upper Great Lakes. After at least 50 years in Lake Ontario, the lamprey made its way into Lake Erie in 1923 where it did not flourish because of the lack of suitable spawning streams and limited deepwater environment. In 1932 the first sea lamprey was reported in Lake Huron; 4 years later the lamprey was in Lake Michigan; and by 1946 the first report was made of a sea lamprey in Lake Superior (Table 6). Three years after the first sea lamprey was reported in Lake Huron, the production of lake trout started to decline (1935), and by 1946 (Table 4) the commercial fishery for this species in Lake Huron proper was finished, although the fishery in Georgian Bay lasted another 9 years. Lake trout production began to decline in Lake Michigan in 1943 (7 years after the first lamprey was reported); by 1950 production dropped below 0.1 million pounds (Table 4), and the species was virtually extinct 3 years later. Only 18 years passed from the time the first sea lamprey was reported in Lake Huron (1932) until the species was commercially extinct in Lakes Huron and Michigan.

The demise of the lake trout population in Lake Ontario and the role of the sea lamprey is more complicated than in the upper lakes. Whether the sea lamprey was endemic to Lake Ontario (Christie, 1972), or became established after the opening of the Erie Canal (Smith, 1974), at least 75 years passed before the lake trout production began its final decline (1928). A substantial fishery continued, however, for another 10-12 years. The species was last reported in the commercial catch statistics as late as 1964 (Baldwin and Saalfeld, 1962, with supplement). That the sea lamprey was a strong factor in the loss of lake trout in Lake Ontario is undisputed; the reasons why the struggle lasted so long remain a subject of speculation.

The sea lamprey's favored prey was the lake trout, but other species as well were victims of this marine invader. Larger individuals of lake whitefish, ciscos, lake herring, suckers, and burbot were attacked by the sea lamprey. The production of burbot (never a prime commercial species) began to decline in Lake Ontario in 1930, in Lake Erie in 1947, and in Lakes Huron and Michigan by 1948 (Table 4). The burbot population became commercially extinct in these lakes about 1960.

Other species also began declining during this period, although the declines were not related to the sea lamprey. The sauger began declining in Lake Huron (primarily Saginaw Bay) in 1935; 2 years later the species was commercially extinct. Beeton (1969) gave the reason for the decline as the development of an environment not suitable for the sauger or the Saginaw

TABLE 6. FISH-SPECIES INTRODUCTIONS IN THE GREAT LAKES BY YEAR AND LAKE, FIRST YEAR OF COMMERCIAL SIGNIFICANCE, AND CURRENT PRODUCTION

Species	First recorded		First reported in commercial catch		Reached commercial significance[a]		1974 Production	
	Year	Lake	Year	Lake	Year	Lake	1,000 pounds	lake
Sea lamprey[b]	1800's	Ontario						
	1921	Huron						
	1936	Michigan						
	1946	Superior						
Alewife[b]	1873	Ontario	?		1920's	Ontario	1,332	Erie
	1931	Erie	?					
	1933	Huron	?					
	1949	Michigan	1956	Michigan	1957	Michigan	45,508	Michigan
	1953	Superior						
Gizzard shad	1900	Ontario						
Coho salmon	1968	Ontario						
	1968	Erie						
	1967	Huron						
	1966	Michigan						
	1966	Superior						
Chinook salmon	1969	Ontario						
	1970	Erie						
	1967	Huron						
	1967	Michigan						
	1967	Superior						
Rainbow smelt[b]	1923	Michigan	1946	Ontario	1952	Ontario	110	Ontario
	1925	Huron	1946	Erie	1952	Erie	15,766	Erie
	1930	Superior	1935	Huron	1950	Huron	215	Huron
	1931	Ontario	1931	Ontario	1933	Michigan	1,748	Michigan
	1935	Erie	1935	Superior	1956	Superior	2,853	Superior
Carp	1885-1895	Ontario	1899	Ontario	1910	Ontario	411	Ontario
	1880-1895	Erie	1892	Erie	1893	Erie	3,152	Erie
	1880's	Huron	1899	Huron	1908	Huron	739	Huron
	1880's	Michigan	1893	Michigan	1903	Michigan	3,244	Michigan
	?	Superior						
Goldfish	?		1929	Erie	1933	Erie	54	Erie
White perch	1950[c]	Ontario	1955	Ontario	1964	Ontario	371	Ontario

[a] Production exceeded 100,000 pounds.

[b] Year of record from Smith, 1972.

[c] Year of record from Christie, 1972.

TABLE 7. FISH-SPECIES IN THE GREAT LAKES THAT HAVE EXPERIENCED SEVERE DECLINES, LAKE AFFECTED, AND SUSPECTED CAUSE OF DECLINE

Species	Principal lakes affected	Primary cause(s) of decline
Atlantic salmon	Ontario	Deterioration and blockage of streams, exploitation
Sturgeon	All lakes	Exploitation, destruction of spawning streams
Lake trout	Erie	Exploitation
Northern pike	Erie, Ontario Huron	Destruction of spawning areas, exploitation
Lake herring	All lakes	Exploitation, environmental changes, competition with introduced species
Burbot	All lakes	Sea lamprey, environmental change
Cisco (chubs)	All lakes	Exploitation, competition with introduced species, sea lamprey
Sauger	Huron, Erie	Environmental change, exploitation
Lake trout	All lakes (except Erie)	Sea lamprey, exploitation
Walleye	All lakes	Environmental changes, exploitation, destruction of spawning streams
Blue pike	Erie and Ontario	Environmental changes, exploitation
Whitefish	All lakes	Environmental changes, exploitation, sea lamprey
Yellow perch	Erie, Huron, Michigan	Competition with introduced species, exploitation, environmental changes
Fourhorn sculpin	Ontario, Erie	Competition with introduced species, environmental change
Emerald shiner	Michigan	Competition with introduced species, environmental change

Bay populations of walleye and whitefish. In Lake Erie the sauger production fell below 0.5 million pounds in 1946 (Baldwin and Saalfeld, 1962) for the first time after nearly 70 years of production between 1 and 6 million pounds. Environmental changes, plus heavy exploitation, were believed to be the causes (Table 7).

The decline of the lake herring, historically the most productive species in the Great Lakes (Smith, 1968), began in Lake Erie in 1925, and by 1963 this fish had become commercially extinct in all the lakes except Superior. Heavy exploitation was undoubtedly a factor in the decline of the lake herring. The role and impact on this decline of introduced alewife and smelt and of environmental factors, however, have not been isolated. The collapse of the lake herring stocks in the mid-1920's was the event most responsible for stimulating interest and concern in the welfare of the Great Lakes aquatic environment. This concern was primarily responsible for identifying the rapid deterioration in the water quality of Lake Erie, which is discussed in a following section.

Water Quality and Population Changes, 1925-1950

Changes in dissolved chemical constituents continued to accelerate after 1925 in all the lakes except Superior (Table 8). The absolute values of these "indicator" chemical parameters are of no toxicological concern, but again the rate of change indicated substantial inputs from cultural and industrial sources. Concentrations of these and other chemical compounds must have been substantial in the receiving waters near the pollution source. The loss of whitefish, lake herring, sauger, and other species from the inner portions of Saginaw and Green Bays due to water quality changes would be expected.

TABLE 8. ESTIMATED AVERAGE CONCENTRATIONS OF DISSOLVED CHEMICAL CONSTITUENTS IN THE GREAT LAKES (EXPRESSED IN MG/LITER)[a] 1950 WITH PERCENTAGE CHANGE SINCE 1925 IN PARENTHESES

Lake	Total dissolved solids	Calcium	Sulphate	Chloride	Sodium and potassium
Superior	56 (-3)	13 (0)	4 (0)	2 (0)	3 (0)
Michigan	150 (5)	34 (0)	17 (31)	5 (25)	-
Huron	110 (2)	24 (0)	13 (44)	6 (50)	4 (0)
Erie	170 (16)	38 (15)	23 (44)	19 (73)	9 (29)
Ontario	172 (15)	38 (12)	25 (39)	19 (73)	10 (43)

[a] From Beeton, 1969.

Population Increases, 1925-1950

The population in the Great Lakes basin had exceeded 18 million by 1950 (Beeton, 1969), an increase of approximately 40% in 25 years (Table 3). Again, the greatest numerical growth was in the Lake Erie basin with an increase from 5.8 to 8.6 million (48%). The population in Lake Erie's basin was 46% of the total population and, combined with the Lake Ontario population, accounted for 62% of the total. The population in the Lake Michigan basin was nearly 5 million in 1950. This continued concentration of people in Michigan, Erie, and Ontario lake basins, with the associated municipal, industrial, and agricultural wastes, was the primary cause of the accelerated rate of increases in dissolved chemical constituents in these lakes.

Lake Erie--Demise is Heralded

The sudden collapse of the Lake Erie lake herring fishery in 1925 awakened the public to the need for scientific investigations into the causes of the precipitous decline. The magnitude of the decline in lake herring production was from an average of 26 million pounds per year in the previous decade to 6 million pounds in 1925, to less than a million pounds in 1929.

Since environmental factors were thought to be the cause of the lake herring decline, two intensive limnological studies (Wright, 1955; Fish, 1960) were initiated in 1928. Wright (1955) found unfavorable conditions in rivers and estuaries, but concluded that environmental changes in the open waters of the western basin of Lake Erie in 1928-30 had no adverse effect on the decline of fish stocks. Fish et al. (1960) also found no environmental basis for the decline of lake herring in the central and eastern basins in 1928-30. Although neither investigator found measurable environmental degradation in the open lake, their studies for the first time established a scientific base line of data on benthic organisms, plankton, and dissolved oxygen. The base line has subsequently been invaluable in measuring environmental changes in Lake Erie.

The effects of the sea lamprey on the lake trout stocks (previously discussed) were recognized in the 1940's, and attempts to control the lamprey began in 1946. Another decade passed, however, before an organized and substantial program was developed to control this destructive parasite.

CHANGE AND REHABILITATION (1950-1975)

Fish Stocks

Changes in abundance of fish stocks are continuing in 1975; however, many changes are now deliberate and controlled. Uncontrollable changes in native species (usually decreasing in numbers) and in introduced species (usually increasing in numbers) frequently occurred during the past 25 years.

1950's

Lake trout production reached zero in Lake Michigan and began to decline in Lake Superior in 1950. Walleye production started to decline in 1950 in Lake Michigan. Cisco (chub) production dropped below 100,000 pounds in Lake Ontario, the first of the lakes to lose its chub population.

In 1952 production of lake herring in Lake Michigan and blue pike in Lake Ontario began their "terminal" decline. Lake whitefish, blue pike, and walleye production began declining in Lake Erie by 1956. By 1959 production had fallen below 100,000 pounds for lake herring in Lake Ontario, Huron, and Erie; sauger in Lake Erie; and blue pike in Lakes Ontario and Erie. Within a few years the blue pike had become virtually extinct in Lakes Ontario and Erie. The emerald shiner, once exceedingly abundant, became extremely scarce in Lakes Michigan and Huron.

Increases also occurred in the 1950's. Smelt production exceeded 200,000 pounds in Lakes Ontario and Huron; 800,000 pounds in Lake Superior; 6 million pounds in Lake Erie; and 9 million pounds in Lake Michigan. The rainbow smelt had become a significant species in the commercial catch of all the lakes in less than 30 years after its introduction in Lake Michigan.

The first alewife was reported in Lake Michigan in 1949, and the species was first reported in the commercial catch in Lake Michigan in 1956. By 1957 production exceeded 100,000 pounds, and by 1958 (9 years after it was first reported) over 1 million pounds of alewives were produced in Lake Michigan. Similar rapid colonization of the white perch occurred in Lake Ontario; only 5 years elapsed between the first record of its presence (1950) and the first report of it in the commercial catch (1955).

1960's

During this decade species of the whitefish family continued to decline in the Great Lakes. Lake whitefish production fell below 100,000 pounds in Lakes Ontario and Erie; lake herring began declining in Lake Superior and fell below 100,000 pounds in Lake Michigan; deepwater cisco (chub) production began declining in Lakes Huron and Superior. Shallow water species also declined: walleyes in Lakes Michigan and Ontario; yellow perch in Lake Michigan; and northern pike in Lake Huron. The fourhorn sculpin, once abundant in Lake Ontario, was extremely rare in the 1960's. A major decline of the fourhorn sculpin during this period was also noted in Lake Michigan (Wells and McLain, 1972).

Rehabilitation of the Fish Stocks

Biologists recognized that rehabilitation of fish stocks, principally lake trout, could not begin until the sea lamprey was brought under control. A special agency, the Great Lakes Fishery Commission, was created in 1956 by a treaty between Canada and the United States to fund and coordinate existing efforts to control the sea lamprey. Initial control methods attempted to block spawning migrations into streams by means of mechanical and electrical barriers. This method proved ineffective. In 1957, after several years of research and testing thousands of chemicals, one was found which was toxic to the lamprey but not lethal to other fish. Treatment of lamprey-infested streams with the chemical 3-trifluoromethyl-4-nitrophenol (TFM) began in 1958. By 1962, 2 years after all known lamprey nursery streams had been treated in Lake Superior, success was verified when the number of adult lampreys at assessment barriers was reduced nearly 85% (Baldwin, 1964). The incidence of lamprey wounds on lake trout dropped sharply, and survival of lake trout increased dramatically in Lake Superior. A method of control had been found just in time to save the last natural population of lake trout in the Great Lakes. The first complete treatment of all Lake Michigan lamprey-infested streams was completed in 1963, Lake Huron in 1970, and Lake Ontario in 1972. Chemical treatment of streams at intervals of 2-4 years must continue, however, if the rehabilitation of lake trout and other species is to become permanent.

The introduction of Pacific salmon in the Great Lakes had been attempted many times, but had produced limited results until the successful introduction of the coho salmon (Oncorhynchus kisutch) in Lake Michigan in 1966. By 1969 coho and chinook salmon (Oncorhynchus tshawytscha) had been introduced into all the upper lakes. The purpose of stocking coho and chinook salmon in the Great Lakes was to increase the sport fishing potential and not to establish self-sustaining populations. "Successful" introduction, therefore, relates to rapid growth and high survival rates. The pink salmon (Oncorhynchus gorbuscha), however, was an "unplanned" plant in Lake Superior, where it succeeded in establishing spawning runs in 1959 and by 1975 had become established in Lakes Huron and Michigan.

Supplemental plantings of lake trout, following lamprey control, have been made since 1958 in Lake Superior. The stocks have been built up to near pre-lamprey levels. Reproduction of hatchery-reared fish has been disappointing, however. Only in the last 2 or 3 years has the outlook improved, when increasing numbers of young native trout have been reported.

The reintroduction of lake trout in Lake Michigan, beginning in 1965, has proved extremely successful in terms of survival and growth. No evidence of reproduction, however, has been reported. Lake trout are now being stocked in Lakes Huron and Ontario. Biologists continue to be optimistic about the reestablishment of self-sustaining populations of lake trout in all the Great Lakes, except Erie.

Salmonids other than lake trout and Pacific salmon have been stocked in the Great Lakes since the lamprey has been controlled. Steelhead trout (rainbow trout), brown trout, brook trout, and Atlantic salmon are now stocked in the lakes. Over 20 million salmonids annually are stocked in the Great Lakes. In 1974 the first experimental plant of hatchery-reared saugers was stocked in Lake Erie.

Environmental Changes, 1950-1975

Scientific investigations of environmental conditions of the Great Lakes have increased exponentially during the past 25 years. Changes in fish populations, benthic organisms, plankton, and water quality are now measured with greatly improved accuracy and frequency. The ability to control environmental conditions and to understand ecological interactions, however, remains a goal of the future.

Chemical changes--The increase in major ions continued in all the lakes except Superior during the last 25 years. The rates of increase in all the ions except calcium remain high for Lakes Ontario and Erie (Table 9). Population increases also were substantial in the basins of Lakes Ontario and Erie (Table 3) and probably account for the chemical changes.

TABLE 9. ESTIMATED AVERAGE CONCENTRATIONS OF DISSOLVED CHEMICAL CONSTITUENTS IN THE GREAT LAKES IN 1970 (EXPRESSED IN MG/LITER)[a] WITH PERCENTAGE CHANGE SINCE 1950 IN PARENTHESES

Lake	Total dissolved solids	Calcium	Sulphate	Chloride	Sodium and potassium
Superior	55 (-2)	13 (0)	4 (0)	2 (0)	2 (-33)
Michigan	155 (3)	34 (0)	20 (43)	7 (40)	5 (0)
Huron	115 (3)	27 (12)	17 (31)	7 (17)	4 (0)
Erie	206 (21)	38 (0)	27 (17)	27 (42)	14 (56)
Ontario	210 (22)	40 (5)	30 (20)	29 (53)	15 (50)

[a] From Weiler and Chawla, 1969.

Critically low dissolved oxygen (DO) concentrations had not been reported in the open waters of the Great Lakes until 1953. In that year Britt (1955) measured DO concentrations less than 1 mg/liter in the western basin of Lake Erie. Although the low DO levels lasted only a few days, it caused a substantial mortality in the burrowing mayfly (Hexagenia) population. In some areas of the western basin the entire population was killed, where more than 1,000 mayfly nymphs per square meter had previously been found (Britt, 1955). The first extensive zone of low DO (less than 1 ppm) was measured in 1959, in the western portion of the central basin of Lake Erie. An interagency synoptic survey of this basin in 1959 found an area of approximately 1,400 square miles which contained less than 1 ppm of DO in the hypolimnion. These conditions of low DO undoubtedly had occurred before 1959 (Carr, 1962).

Dissolved oxygen levels of less than 1 mg/liter occur annually in the bottom waters of the central basin of Lake Erie and by 1974 covered several thousand square miles. Oxygen depletion also has been reported in southern

Green Bay (Lake Michigan) and the Bay of Quinte (Lake Ontario). Low DO levels in the open waters of the other lakes have not been reported. The virtual extinction of the sauger and blue pike and the decline of the walleye population in Lake Erie are thought to be partially caused by the low DO conditions (Smith, 1974).

Toxic Substances in Fish

Chemical contaminants in Great Lakes fish have been measured with increasing frequency in the past decade (1965-75). Measurements were first made in 1965 of the residues of the insecticides DDT and dieldrin in Great Lakes fish. All 28 species for which DDT and dieldrin analysis has been made contained measurable levels. Several species (chubs, lake trout, lake herring) from Lake Michigan exceeded the U.S. Food and Drug Administration's (FDA) tolerance level of 5 μg/g in fish used for human consumption (Reinert, 1970). Since the use of DDT was banned in 1972, the level in Lake Michigan fish has decreased rapidly, from an average of 10 μg/g in bloater chubs before 1972 to less than 3 μg/g in 1974.

During the same period in which DDT levels were decreasing in Great Lakes fish, polychlorinated biphenol (PCB) levels were increasing. Again, the species containing the highest levels were lake trout and bloater chubs in Lake Michigan. The average concentration of PCB in Lake Michigan lake trout above 24 inches exceeded 20 μg/g in 1974. Concentrations above the FDA's 5 μg/g tolerance level have been reported in fish from Lake Ontario and Lake Huron, as well as Lake Michigan.

In 1969 mercury levels in excess of the FDA's tolerance level of 0.5 μg/g were discovered in several species of fish (including walleye and white bass) from Lakes St. Clair and Erie. Mercury levels above 0.5 μg/g were also reported from Lakes Superior and Ontario. Two years following curtailment of the source of mercury pollution to Lake St. Clair, the levels in fish began to decrease. In two instances (DDT and mercury) stopping the sources of chemical contaminants resulted in the rapid decline of the toxicants in the environment. This success should give support to continued efforts to solve problems by eliminating the direct cause.

The contamination of Great Lakes fish with levels of DDT, PCB, and mercury exceeding the FDA tolerance level has resulted in great financial hardship to the commercial fishing industry. Direct or even indirect adverse effects on the fish populations of the Great Lakes have not been detected. Apparently, DDT and PCB in the low nanogram-per-liter levels in the open lake waters have, through biomagnification, reached the microgram-per-gram level in fish tissue.

Changes in Benthos and Plankton

Changes in bottom-dwelling organisms have been documented by several investigators within the past 20 years: Britt (1955) and Carr and Hiltunen (1965) for Lake Erie; Schneider, Hooper, and Beeton (1969) for Saginaw Bay; Hiltunen (1967) for Lake Michigan. In all of these studies the changes have been from the more "pollution-intolerant" organisms (mayflies, caddisflies, amphipods) to "pollution-tolerant" forms (primarily oligochaetes and midge larvae) and from greater to lesser species diversity. The geographic areas affected by loss of intolerant organisms are being extended further into the lakes from the pollution sources (primarily river mouths). The effects of these changes on fish populations will remain speculative until the interactions can be quantitatively assessed.

Phytoplankton and zooplankton populations have also changed markedly in many areas of the Great Lakes (Beeton, 1969). The changes in phytoplankton have been from dominance by multispecies diatom communities to species of green and blue-green algae more tolerant of eutrophic conditions. Zooplankton communities have reacted similarly (Beeton, 1969), resulting in a loss of species diversity and increases in species associated with eutrophic environments. Again, the relation of these changes in fish populations is incompletely understood.

CONCLUSIONS

It is obvious that the environment in many areas of the Great Lakes has deteriorated. Assigning direct cause and effect to changes in specific populations or species of Great Lakes fish is difficult and controversial. Heavy exploitation of many stocks is undoubtedly a factor in the decline of many species. Changes in water chemistry, plankton, bottom fauna, and unexploited fish species, however, clearly show that factors other than fishing have drastically changed the characteristics of the Great Lakes.

Now that we know our capabilities, how can we avoid past mistakes and stop, or perhaps even reverse, the trend toward environmental chaos? One possibility is to understand the forces that operated in the past to produce present conditions. Scientists and administrators with responsibility for protecting the aquatic environment can learn much from the perturbations foisted on the Great Lakes. For example, early recognition of the effects of unmanaged commercial fishing could have prevented, or at least delayed, the decimation of many fish populations. Wise management of the uses of tributary streams would have saved many stocks of anadromous species. It is difficult, however, to blame these errors of omission on our predecessors, for they did not have the advantage of hindsight to improve their foresight. Our generation has no such excuse. Opportunities missed in the past to protect the aquatic communities are gone, but opportunities remain to save and rehabilitate our aquatic environment.

Recognition of environmental degradation in the Great Lakes has led Canada and the United States to a firm commitment to halt and reverse this trend. Evidence of success in this endeavor is already apparent. Rehabilitation of many tributaries has permitted the establishment of spawning runs by anadromous species. Levels of DDT in fish tissue have decreased as much as 80% after the use of the insecticide was banned. More comprehensive and better treatment of municipal and industrial waste has resulted in noticeable improvements in the quality of receiving waters.

Let us hope that by the year 2000 the history of changes in fish species of the Great Lakes will show only increases in native species between 1975 and the new century.

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An Airlift Sampling Device for In Situ Collecting of Biota from Rocky Substrata

James R. Chess
National Marine Fisheries Service
Southwest Fisheries Center
Tiburon, California

INTRODUCTION

Problems inherent in collecting organisms from the rocky sublittoral zone have undoubtedly limited study of this habitat. Most investigations of benthic biology have dealt with assemblages of organisms on soft or unconsolidated substrata, a fact reflected in the list of marine bottom samplers compiled by Hopkins (1964), where only 3 of 107 devices are capable of sampling (only qualitatively) rocky substrata. The inadequacy of this sampling capability has become obvious with the recent need to produce environmental impact statements as a prerequisite to construction and to other activities in the coastal zone. Typically the quality and comparability of the data generated by these studies have been limited by lack of adequate standardized sampling equipment and procedures.

This report describes a driver-operated airlift sampling device designed to collect organisms on rocky substrata. It is inexpensive but durable, made of readily available materials, and requires neither special talents nor tools for construction or operation. Most important, with it quantitative samples can be taken. I designed the prototype of this airlift in 1967 during studies of benthic assemblages at the USFWS Sandy Hook Marine Laboratory, Highlands, N.J. It was later tested and modified during three years of intensive study of the benthic biota at Catalina Island, California (Hobson and Chess, in prep.). The only limitations found were in sampling forms that were either very motile (e.g. some fishes), deep burrowing, or strongly attached to the substrata.

Sampling devices using the airlift principle are not new. They have taken diverse form, but have the following characteristics in common: Air is introduced into the lower end of a submerged tube and mixes with the water as small bubbles. The specific gravity of the mixture is so reduced that the pressure of the water outside the tube causes the mixture to overflow at the top and suction to develop at the bottom opening. Thus, the device can be used much like a vacuum cleaner, collecting organisms in a bag at the upper end (Figure 1).

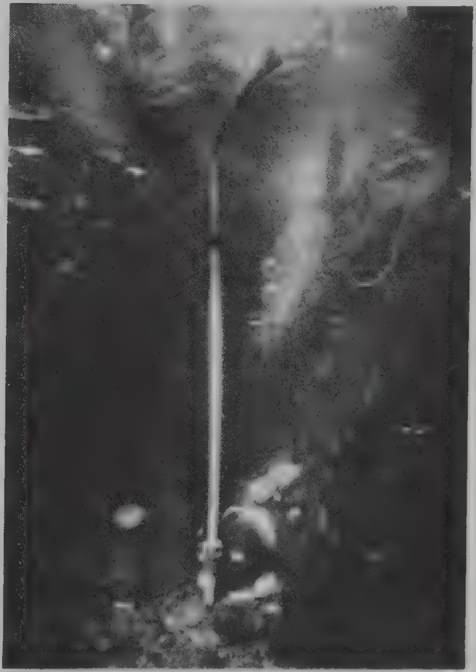

Figure 1. Airlift Sampler in operation.
(Photo by Edmund S. Hobson)

Airlift samples have been used by Barnett and Hardy (1967) to collect deep burrowing clams, by Emery (1968) to collect plankton, and by Chesher (1969) to collect spatangoid echinoids. These devices, however, are differently designed and are less versatile than the airlift described here. Several groups of investigators on the west coast are currently using airlift samplers based on the design described below.*

DESCRIPTION OF THE APPARATUS IN OPERATION

The major element of the airlift sampler (Figures 1 and 2) is a 3 m length of 55 mm I.D. schedule 40 Polyvinylchloride (PVC) pipe. The pipe is held vertical in the water by a buoy attached near the upper end and enough weight attached near the intake end to create about 1kg negative buoyance.

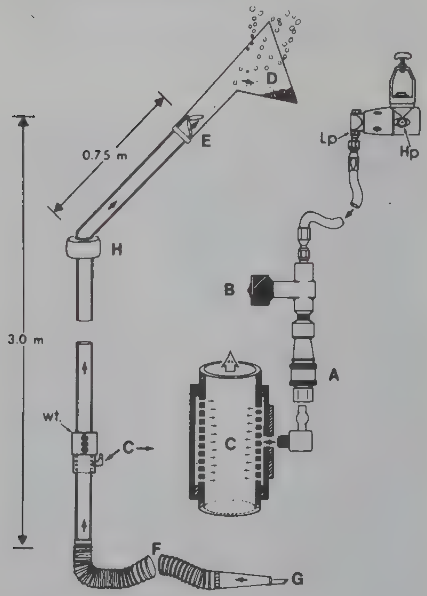

Figure 2. Diagramatic representation of the Airlift Sampler: A) Quick-disconnect coupling; B) Airflow control valve; C) Manifold; D) Collecting bag; E) Flap valve; F) Shop vacuum cleaner hose; G) Scraper attached to nozzle; Lp: Low pressure outlet; HP: High pressure outlet; wt; weight.

The air supply can come from 1) the operator's own air supply via hose from a second low pressure outlet of his scuba regulator, 2) an air supply on the surface, or 3) a separate air tank and scuba regualtor carried by the operator. The latter method seems best for most sampling applications. An air hose 2 m in length is attached to the low-pressure outlet of the regulator (approx. 100 psi) and is connected to the sampler by a stainless steel quick-disconnect air-hose coupling (Figure 2A). An airflow control valve is placed in the hose before the coupling (Figure 2B).

Air is introduced into the pipe through 1 mm perforations within the air manifold (Figure 2C) near the lower end of the pipe. The manifold, constructed of a 10 cm length of 75 mm I.D. PVC pipe, is glued around the perforated portion of the pipe. Spacers placed at each end of the manifold create a 6 mm gap between the pipe and manifold, allowing distribution of air to all of the perforations.

When the sample is carried up the tube it is collected in a removable mesh bag fitted over the tube's upper opening (Figure 2D). The bag is designed to allow the air to escape readily yet retain the sample.

The upper 75 cm of the pipe is offset at a 45° angle, and its opening into the bag is fitted with a flexible flap valve (Figure 2E). Both features prevent material from falling back down the tube. The angled portion of the pipe also directs the flow of water and fine sediments (which pass through the mesh) away from the sampling site, thus reducing the amount of materials that would otherwise fall on the operator. The structure of the collecting bag and the offset angle of the tube also tend to prevent the bag from draping over the opening when heavy materials are collected.

SAMPLING PROCEDURES

Sampling Easily Accessible Horizontal Surfaces

Various large organisms such as certain asteroids, echinoids and molluscs cannot be collected by the airlift, and are usually removed from the sample area by hand after being identified and enumerated.

Many motile forms, including various shrimps and small fishes, can be captured by first passing the airlift intake carefully over the sample area, working from the periphery inward to reduce escapement. The substrate is then scraped with a sharpened tool, such as a stiff putty knife, while holding the intake end of the pipe a few cm above. The sessile organisms and associates are drawn up the tube and into the collecting bag. Other tools such as small picks and scrapers of various design are useful when collecting cryptic forms on substrata with many interstices; the quality and completeness of a sample is largely dependent upon how thoroughly the substrate is cleaned.

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*Organizations known to be currently using airlift devices of the design described in this report include National Marine Fisheries Service, the University of Southern California, Scientific Application Inc., U.S. Bureau of Land Management, Dames and Moore, Marine Biological Consultants, Inc., University of Alaska, and Alaska Coastal Research.

Sessile organisms which are firmly attached to the substratum, such as serpulid polychaetes and molluscs, as well as rock borers, are often difficult or virtually impossible to collect quantitatively. Those that remain on the sampled substrata after the collection are, to the extent possible, identified and enumerated.

Sampling Surfaces Inaccessible to Standard Procedures

Surfaces inaccessible to the standard procedure—vertical surfaces and beneath overhangs, where it is difficult to maintain position—can often be sampled by attaching a flexible corrugated shop vacuum cleaner hose to the intake end of the pipe (Figure 2F). (Remember that the pipe must remain near vertical to operate satisfactorily.) A scraper attached directly to the nozzle of the hose (Figure 2G) is effective for collecting organisms in crevices, holes and areas where the operator cannot use both hands.

Sampling Soft Substrata

Assemblages of organisms associated with soft substrata can be quantitatively sampled by first pushing an open-ended cylinder or cofferdam into the substrata, and then collecting the contents to the desired depth. This procedure has limitations and problems, however. If the sediments do not pass through the mesh, they will be retained in the bag, and its weight may tilt the pipe to the horizontal, at which position it ceases to operate. Furthermore, when collecting organisms frome coarse sand substrata, mysidaceans, small polycheates and other fragile organisms tend to become macerated by the sand that accompanies them up the tube.

A seived sample may be obtained if the sediments are fine enough to pass through the mesh of the collecting bag. This is possible, however, only when the sediment is drawn slowly up the tube, a small amount at a time, to avoid its accumulation in the bag.

Miscellaneous Aspects of the Airlift Operation

- The efficiency of the airlift increases with decreasing size of the bubbles entering the lumen of the tube (a fact related to the greater surface to volume ratio of small spheres). Reduced bubble size is a function of the small perforations in the tube within the manifold.

- A small amount of airflow up the pipe is sufficient for most applications. A typical 0.25m² quadrat can be sampled in 10 to 15 minutes, and the material from 2 to 6 quadrats can be collected with the air contained in a standard 72 ft³ compressed air tank, depending upon water depth, type of substrata and the efficiency of the operator.

- Generally it is preferable that the airlift be accompanied by a separate tank and regulator. An independent air supply provided by additional air tanks can be made available when necessary, and the operator can leave the unit on the bottom to attend to other tasks unencumbered. When air is supplied to the airlift from the operator's own supply, or from the surface, the operation becomes either less efficient or more complicated, or movement is restricted. Under certain circumstances, however, when the airlift operation requires more compressed air, and extensive mobility is unnecessary, a surface air supply might be more expedient. On the other hand, in operations that require mobility but need only a small volume of air, the operator might find advantage in using air from the scuba system supplied for a second low-pressure outlet of his regulator.

- The fine mesh in most collecting bags tends to inhibit the escapement of air, thus reducing the efficiency of the airlift. Bags of the design illustrated in this report, however, make it possible to use mesh sizes as small as 0.25 mm and still have adequate air passage. Escapement of air from the bag is increased by a localized pressure differential established within an enverted conical air chamber formed in the uppermost corner. Nitex* material with 0.333 mm mesh was used in fabricating these bags, but 0.5 or 1.0 mm material would be more compatible with most other sampling procedures.

- Increasing the vertical stability is helpful where currents or surge are strong. This can be achieved by attaching additional or larger buoys and weights to the top and bottom of the unit. If a doughnut-shaped buoy is used, it can be fitted around the pipe and slid down to the weighted end when the device is to be moved. The vertical stability is thus lost and the pipe easily tilted to the horizontal where it is more portable for a swimmer.

- Although the efficiency of an airlift pipe is generally directly proportional to its length, longer pipes are in most cases more awkward to handle. Although short airlift tubes use more air for a given amount of work, they operate satisfactorily. Jeffery G. Grovhoug, (Naval Under Sea Center, Hawaii, pers. comm.), used a tube 127 cm in length and 10 cm I.D. to sample in depths as shallow as 1.5 m. An airlift can be fabricated in sections for easy transport and for changing its length for use at various depths. An overall length of 3 m seems to be a good compromise between reasonalbe mobility and efficiency.

- At greater depths the efficiency of an airlift is reduced because increasing amounts of compressed air are required to drive the unit. Also the ratio of hydrostatic pressure between both ends of the vertical pipe decreases with depth. At depths where most divers work, however, this reduction in efficiency is negligible. The airlift described in this report has worked satisfactorily to depths of 40 m.

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James R. Chess is a Fishery Biologist (Research) at the Southwest Fisheries Center, Tiburon Laboratory, California. His research has centered on interrelationships of invertebrate communities and predatory fishes. He holds a degree from Humboldt State University and has authored and coauthored several papers on the natural history and ecology of marine organisms.

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*Note: Reference to trade names does not imply endorsement by the National Marine Fisheries Service (NOAA).

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SYMPOSIUM ON FISH UTILIZATION TECHNOLOGY AND MARKETING IN THE IPFC REGION

Manila, Philippines, 8-11 March 1978

THE PROBLEM OF BURNT TUNA IN THE HAWAIIAN FISHERY

by

Jean I. Cramer*, Richard S. Shomura, and Heeny S.H. Yuan
Southwest Fisheries Center
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96812

Abstract

The poor quality of flesh in "burnt tuna" results in economic loss to the tuna industry. Rejection of burnt tuna by the consumer is based on visual and taste shortcomings. The present report describes the status of this problem in the Hawaiian tuna fishery and provides some preliminary results of an on-going study to understand the phenomenon.

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*Part of study done under contract with the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, Hawaii

Introduction

Tunas represent the most important economic fishery resource in the Hawaiian Islands. In 1976 the total domestic tuna catch was 5,550 metric tons (MT) with an ex-vessel value of $6.4 million (U.S.). While skipjack tuna, Katsuwonus pelamis, was the most important species in the tuna catch, making up approximately 80% of the landings and 60% of the value, the importance of the other tuna species, especially yellowfin tuna, Thunnus albacares, and bigeye tuna, T. obesus, has increased markedly in recent years. Table 1 provides catch statistics of the tunas for the 1962-76 period. The increase in landings of the combined yellowfin tuna, bigeye tuna, albacore, T. alalunga, and kawakawa, Euthynnus affinis, catch has been due primarily to the expansion of the handline fishery for tunas and the increase in recreational fishing. Recreational fishing in Hawaii has a unique aspect in its operation, wherein the economically valuable species are very often sold through commercial outlets. Basically the operation is still considered recreational fishing since the fishers do not depend upon fishing as a basic means of livelihood.

Economically, the handline fishery for tunas show a potential of tremendous growth if the problem of burnt tuna can be overcome. The present report provides (1) a brief description of the various types of flesh quality problems faced by the tuna industry, (2) a brief description of the handline and troll fisheries in Hawaii, and (3) results of a current study being undertaken by the Honolulu Laboratory (Southwest Fisheries Center, National Marine Fisheries Service) and the University of Hawaii to determine the causative factors involved with burnt tuna and to seek solutions to this costly problem.

Flesh Quality Problems in Tuna

Burnt tuna is raw tuna which is paler and softer than normal. The color may vary from slightly pale (borderline burn) to almost white. The area affected varies from 5% to 100% of the edible meat of the fish. In cases of partial burn the area affected is the part of the meat which is closest to the spinal column. The condition occurs most frequently in large tunas (yellowfin and bigeye) from 45 to 136 kg caught in shallow water. The fish is edible but is less desirable for raw consumption and therefore commands a lower price.

Burnt tuna appears to be similar to a condition in pork known as Porcine Stress Syndrome (PSS) (Hugh 1976). Both conditions involve stress, high body temperatures, acidity of muscle, and result in pale and soft muscles.

Tuna, along with saury, seerfish, butterfly kingfish, and mackerel, normally contain large amounts of free histidine in their muscle tissue. Under certain conditions the free histidine may be decarboxylated by some bacteria to produce high levels of histamine (Geiger 1944; Kimata and Kawai 1953; Ferencik 1970).

Growth of histamine producing bacteria was optimum at acidic pH (5-6) and moderately high temperatures (20°-30°C) (Kimata and Akamatsu 1955).

One of the best methods of retarding bacterial histamine formation in fish is storage below freezing (Brown and Arnold[2]).

Scombroid fish poisoning clinically resembles histamine poisoning intoxication, however, controversy exists as to whether histamine ingested orally is toxic (Halstead 1967; Granerus 1968; Douglas 1970). A number of reports indicate that histamine taken orally by human subjects is not toxic (Granerus 1968; Douglas 1970; Hardy and Smith 1976). Certain diamines (e.g., putrescine) may alter absorption of histamine (Parrot and Nicot 1965; Irnistea 1973). Alterations of conditions of the intestinal tract due to consumption of highly seasoned hot dishes or alcohol may cause increased absorption of histamine (Geiger 1955). Whether histamine is the sole toxic factor or not, it is generally found at high concentrations in foods causing scombroid poisoning (Simidu and Hibiki 1955; Ferencik 1970).

Honeycombing is a condition which becomes noticeable after precooking in canned tuna. It is characterized by irregular holes or pits penetrating more or less deeply into the tissue. The size of the honeycombed pits may vary from small pits to pits covering extensive areas. A transverse section of an extensively honeycombed area has an appearance suggestive of an empty honeycomb (Hillig 1956). Fish in this condition are rejected for human consumption.

Otsu (1957) reported that honeycombing in Hawaiian skipjack tuna resulted from delayed refrigeration and was independent of sexual maturity or size of fish. The rate of honeycombing increased with higher seawater temperatures. When allowed to decompose to varying stages yellowfin tuna and skipjack tuna with honeycombing had much higher histamine levels than similar fish without honeycomb (Williams 1954).

Studies presently in progress, however, indicate that honeycombing and histamine production are not interdependent. Fish incubated in the presence of antibiotics exhibit honeycombing but do not have high histamine levels (H. Frank, Department of Food Science, University of Hawaii, Honolulu, Hawaii 96822, pers. commun.)

Green tuna occasionally occurs in precooked tuna when the normal pink color fails to develop. The cooked meat takes on a tannish-green color and is rejected as unsuitable for canning (Brown, Tappel, and Olcott 1958). The pink has been shown to be due to a hemochrome derived from the myoglobin in the loin (Brown and Tappel 1957) and the green is mostly hemichrome (Brown et al. 1958; Naughton, Zeitlin, and Frodyma 1958). The condition does not appear to be related to oxygen starvation during landing (Naughton et al. 1958). Green tuna is most frequently found in yellowfin tuna.

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[2] Brown, W. D., and S. H. Arnold. 1957. Histamine (?) toxicity from fish products. Unpubl. manuscr. Institute of Marine Resources, Department of Food Science and Technology, University of California, Davis, California.

The condition is not recognizable in the raw state and therefore much effort is wasted in processing the fish. Nagaoka, Yamagata, and Horimoto (1971) have developed a method for prediction of green tuna. They report that the determination of trimethylamine oxide and trimethylamine contents in the raw dorsal muscle of yellowfin tuna yields a predictive accuracy of 96%.

Description of Fisheries

The problem of burnt tuna seems to be most serious with tuna caught by trolling, serious with tuna caught on night handlines, and minor with tuna caught on longlines. The problem, in fact, was first brought to the attention of the National Marine Fisheries Service by recreational fishers who troll in the Kona, Hawaii area.

Recreational fishers use rods and reels as fishing gear. They troll lures from a wide variety of boats which range in length from 4 to 18 m. The prime target species are the larger game fish, including yellowfin tuna; blue marlin, *Makaira nigricans*; striped marlin, *Tetrapturus audax*; black marlin, *M. indica*; shortbill spearfish, *T. angustirostris*; sailfish, *Istiophorus platypterus*; mahimahi, *Coryphaena hippurus*; and wahoo, *Acanthocybium solandri*. Trolling speed is a matter of individual preference and generally ranges from 10 to 20 km/h. Surface water temperatures in the Kona area where the burn problem is most serious vary between 24° and 29°C.

Lines of various sizes are used on the reels. The heaviest line used has a breaking strength of 59 kg or less. Fishers use lighter lines to make fishing more sporting and challenging. Fighting time, the interval between the taking of the lure by the fish and the boating of the fish is highly variable. In the catching of yellowfin tuna, fighting time is partly a function of line strength and fish size. In a sample of 44 yellowfin tuna caught on line with a breaking strength of 36 kg or less, fighting time ranged from 4 to 198 min with a mean of 46 min. The fighting time in a sample of 29 yellowfin tuna caught on line of 23 kg or less breaking strength ranged from 5 to 329 min with a mean of 93 min. Fish in this sample weighed 46.3-115.2 kg. These variables do not account for all of the variability in fishing time. Fishing technique, skill of fishers, vitality of the fish, weather conditions are conceivably other factors.

Another fishery in which burnt tuna is a serious problem is the night handline fishery for tunas. To our knowledge this highly effective method of fishing for tunas is used only on the island of Hawaii and in the Philippines (E. Oswald, South China Seas Fisheries Development and Coordinating Programme, Makati, Rizal, Philippines, 1976, pers. commun.). Until 1976 this method of fishing in Hawaii was limited to a small area off Hilo, Hawaii. Night handline fishers presently fish in areas off the coastline of the entire southern half of the island of Hawaii.

Fishers time their trips to arrive on the fishing grounds at sundown. Upon arrival the engine is shut down and a parachute is attached to the bow and lowered into the water. The parachute is 7.2 m in diameter. Over surface lights and/or an underwater light are turned on. Typically 25- and 50-W incandescent bulbs are used for the above surface and underwater lights, respectively.

The stage is finally set for fishing with the tossing overboard of a few kilograms of chum consisting of chopped up mackerel scad, Decapterus pinnulatus. If fishing is in an area where the squid, Notodarus hawaiiensis, is expected to be available, then fishing for squid to be used as bait is begun. Otherwise, mackerel scad is used for bait and fishing for tuna commences.

The handline for tuna fishing consists of a hook of Japanese design (Tonkichi BKM No. 54[3]) at one end attached to a leader of about a meter of 7-strand stainless steel wire of 227-kg (500-lb) test, a lead weight of 227-397 g (8-14 oz), and 110-130 m of line which is usually polypropylene rope either 0.95 cm (3/8 in.) or 0.79 cm (5/16 in.) in diameter. At the start of fishing three handlines are set, one at the bow, one at the stern, and one amidship. As soon as the tuna start biting one line is removed and only two lines are fished. The baited hooks are lowered 20-30 m below the surface and held at that depth by securing the handline to the boat with a restraining line. The restraining line usually breaks when a tuna takes the hook. The restraining line has a breaking strength of about 45 kg (100 lb). This high breaking strength is used to increase the probability that the tuna will be securely hooked when it strikes.

After the restraining line breaks the tuna pulls out the handline at great speed. In a few seconds the drag of the increasing amount of line in the water slows the tuna down. When the outgoing line is slow enough the fisher grabs it and hauls the fish to the boat. When the fish is alongside, it is shot in the head, with either a handgun or bang-stick, hit again on the head with a baseball bat, gaffed, and pulled aboard. The catch is stored in ice or a mixture of ice and seawater.

The fishers leave the fishing ground to arrive at the auction site by 7 a.m. When fishing distant grounds they unload their catches at the nearest landing and truck the fish to the auction market.

The fishery catches bigeye tuna and yellowfin tuna primarily. Albacore is a third tuna species that is commonly caught. The contribution of these species to the handline fishery catch in weight and in value for the years 1973, 1974, and 1975 are listed in Table 2. The catch increased from 89.1 to 154.6 MT during these years, while the value of the catch increased at a slightly faster rate, from $141.1 to $327.5 thousand (U.S.).

Although the total tuna catch exhibited a continuous growth for the 3 years, the catches of the individual species fluctuated tremendously between years. In 1974 the bigeye tuna was almost twice as much as the other 2 years; in 1975 the yellowfin tuna catch was more than three times the amount of the previous 2 years, and the albacore catch in 1975 increased by fiftyfold.

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Serious economic losses due to burnt tuna are incurred by night handline fishers. Rebates on burnt fish were reported to range from 5% to 75% of the original auction price of the fish. Annual loss to night handline fishers due to burnt tuna has been estimated to be as high as 16% of their 1976 catch. Other economic losses include the shipping costs incurred and the inevitable poor reputation that the catch of the night handline fishery engenders due to the inconsistent quality.

Possible Causative Factor in Tuna Flesh Quality

Tunas are unique among fishes in that they are "warm bodied" and excess (above ambient water temperature) body temperatures up to 15°C have been reported. Body temperatures of decked bluefin tuna, *Thunnus thynnus*, were reported to be 5° to 15°C above ambient water temperature (Carey et al. 1971). Dizon, Brill and Yuen (in press) telemetered deep body temperature from free swimming skipjack tuna and found mean body temperatures to be higher than the ambient water temperature. Maintenance of body temperature above ambient water temperature is possible due to the presence of rete mirabile (Carey 1973).

The rete mirabile or "wonderful net" is a tissue composed of closely intermingled veins and arteries which permits the free flow of blood for transport of oxygen and other molecules but impedes the flow of heat from the body tissues to the gills. This conservation of body heat allows the tuna some of the advantages of a homeothermic animal. The higher body temperature increased the speed of metabolic reactions thus making possible a higher maximum swimming speed (Carey 1973). The ability to conserve heat and metabolize rapidly, however, produces the possibilities of overheating and rapid accumulation of metabolic by-products.

These relatively high body temperatures and high metabolic rates may be responsible for meat quality problems such as honeycombing, green tuna, and burnt tuna which are unique to tuna.

Devices to Reduce the Incidence of Burnt Tuna

Fishers have tried various methods to eliminate the burnt tuna condition from developing. Some insist that bleeding the fish before chilling is effective. Others advocate precooling the fish up to an hour by leaving it on deck at night or by placing it under burlap and running seawater over it during the day before placing it in the icebox. No method, however, meets with universal acceptance as the solution to the problem of burnt tuna.

In addition to the fishers' attempts three devices have been made to alleviate the problem. One of them has yet to be tried in Hawaii. Use of the other two has been very limited and, to our knowledge, discontinued.

On the assumption that the burnt condition was caused by improper cooling, the Honolulu Laboratory of the National Marine Fisheries Service distributed for trial a device to hasten the transfer of heat from the warmest part of the fish. The device which had the general shape of a comb consisted of five aluminum baking potato nails (11.7 cm long) held together in a row by an aluminum bar 1 x 1 x 14 cm. Three to five of these were inserted on each side into the dark red flesh that runs longitudinally beneath the lateral line in the section of greatest girth.

After one of the night handline fishers of Hilo tried the device, the others refused to use them. They based their refusal on the following reasons: inserting the devices would require too much time; the bars would not be flush with the body contours and would thus snag and tear the flesh; bacteria would be introduced; and, buyers would not buy fish with holes even if the holes are in flesh that is normally discarded. On the other hand, a small group of fishers in the Kona district have used the device until the supply was depleted due to attrition. Use of the device was reported by one fisher to have decreased the incidence of burnt tuna; this fact has yet to be substantiated.

In November 1975 a Mr. Ogawa of Daiichi Suisan Tsukyi, Japan, demonstrated the use of a metal rod to enhance the chilling of tuna. The demonstration was conducted on the island of Hawaii. The tail of the fish was cut off and a rod approximately 3 mm in diameter was inserted the full length of the vertebral column. The insertion was accompanied by deep incisions immediately posterior to the pectoral girdle and slashing of the gills to bleed the fish. Fishers have resisted using this method because of the work involved.

In September 1977 Mr. Haruyoshi Taniguchi, a recognized tuna expert from Japan, described a tool he has developed to instantly kill tunas. The tool consists of a coring cylinder and a stainless steel wire around which a copper spring is wrapped. The coring cylinder is used to bore a hole into the fish's head at the foramen (whitish spot on the middorsal line just above the eye). A length of wire is inserted through the hole and pushed through the spinal column at least 30 cm. This tool reportedly prevents burnt tuna by quickly destroying the nervous system and thus preventing any further stimulation of physiological activity. This method has not been tested in the Hawaiian Islands (Suisan Sekai 1977).

Study of Causative Factors of Burnt Tuna

A preliminary study was conducted in the fall of 1977 to investigate environmental and physiological factors causing the burnt tuna condition and to investigate the similarities of burnt tuna to PSS in swine.

Data were collected at the Hilo fish auction and on a number of night handline boats. Chilling methods used by individual night handline boats were noted whenever this information was volunteered. The senior author made nine trips on seven different boats. The size of the chill box and pounds of ice on board were recorded for each trip. When a large tuna was caught a blood sample was taken by cardiac puncture and the fish was labeled by clamping an ear tag on the pelvic fin.

Immediately after catching and prior to auctioning the superficial and deep muscle temperatures were taken by inserting an 11 cm probe attached to a telethermometer through the skin of the fish along the midline approximately 11 cm posterior of the pectoral fin. Superficial temperatures were taken at a depth of 1/2 cm and deep temperatures were taken at a depth of 11 cm unless the backbone prevented insertion to that depth. Sex was recorded if the belly was slit and the gonads were exposed at the time of auction. Observations were made of all large tuna which were cut on the auction block. The head and tail were cut off and then the fish were quartered. If burn was present, it was recorded.

Samples of tuna meat were obtained at the Honolulu fish auction. These samples were subsequently classified by the researcher as badly burnt, burnt, or not burnt (normal). Two-gram sections of these samples were placed in 10 ml of distilled water and ground up. The pH of these homogenized samples was then determined. Samples of burnt and normal tuna were assayed for lactate and cultured to determine general bacteria levels.

Samples were also obtained from various parts of a small yellowfin tuna which died during a stress experiment at the Kewalo Research Facility. The pH of these samples was determined using the method described above.

Analysis of variance was used to determine significance of temperature differences between chill techniques and between burnt and normal tuna. The volume of the blood samples collected was not adequate for analysis.

Chill methods

A variety of methods is used to chill fish on the night handline fishing boats. The methods vary in the kind and amount of ice used, mixture of the ice with seawater, location and number of cuts for bleeding, and amount of time the fish is on deck between catching and chilling. Cuts for bleeding were usually at the heart, the belly, or the tail.

Five methods of handling are described in Table 3. Deep and superficial temperatures of all tuna over 45 kg were taken at the Hilo auction from 20 September to 15 October 1977 (Table 4). The superficial and deep muscle temperatures of fish were analyzed to determine if significant differences in temperatures exist between chilling techniques (Table 5). Significant differences in superficial temperatures were found between various chilling techniques. Significant differences, however, were found only in the deep temperatures for two pairs of methods (A and D, C and D). The amount of ice carried is probably the most important difference between methods. Deep temperatures were also affected by the amount of time the fish were kept in the chill box. Fish caught early in the evening have a considerably cooler deep temperature than fish caught in the morning.

No significant differences were found between auction temperatures of burnt and normal fish which were quartered at the Hilo auction (Table 6).

Tissue acidity

The stress of catching may result in acceleration of biochemical activity which will lead to an abnormally low tissue pH, premature rigor mortis, short duration of rigor mortis, and early deterioration of tissue (Borgstrom 1961). Differences in pH of burnt and normal tuna from the Honolulu auction were observed (Table 7). Burnt fish appeared to be consistently more acidic than the normal fish.

Conclusions

Burnt tuna is a system which is the result of two classes of factors, physiological stress and postmortem handling, acting independently or in combination. It appears that physiological stress alone may result in a burnt condition. All methods of chilling including immediate rapid chilling on longline boats result in some percentage of burnt tuna. The burnt condition has been observed immediately after catching (V. Ohai, Oceanic International Corporation, Honolulu, Hawaii 96817, 1977, pers. commun.).

It is not clear whether postmortem handling alone may result in burnt tuna or whether prior physiological stress is a necessary precondition. In any case postmortem handling seems to influence the severity of the condition. High levels of bacteria were found in cultures from both burnt and normal tissue samples. The level of bacterial activity may be affected by handling.

It would be very desirable to create an objective classification system for burnt tuna both from a research and an economic point of view. A color wheel could be developed which would allow an objective classification system for degree of burn of quartered tuna. It may be possible to detect burnt tuna by use of a tissue pH probe. If good correlations are found among the color wheel, visual classification system, and internal pH taken by the probe, a reliable system of grading uncut tuna may be developed.

Further evidence is necessary to confirm that a malignant hyperthermia is involved. It is also possible that an injection of a buffer such as bicarbonate may be used to counteract the effects of stress.

Current efforts in burnt tuna research are concentrated in the following areas: (1) continued investigation of the effects of catching and chilling techniques on the incidence of burnt tuna, (2) investigations into biochemical, histopathological, and microbial differences between normal and burnt tuna immediately after catching and after chilling, and (3) development of an objective classification system for burn in whole uncut tuna.

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Table 1.--Tuna catch, State of Hawaii.

Year	Skipjack tuna		Yellowfin tuna		Bigeye tuna		Albacore		Kawakawa	
	Weight (MT)	Value (thousands of US$)	Weight (MT)	Value (thousands of US$)	Weight (MT)	Value (thousands of US$)	Weight (MT)	Value. (thousands of US$)	Weight (MT)	Value (thousands of US$)
1976	4,445	3,827	840	1,673	197	825	27	40	41	23
1975	2,293	2,282	781	1,371	157	673	43	83	30	16
1974	3,374	2,676	523	983	187	731	9	15	16	9
1973	4,878	3,203	349	625	185	688	14	28	15	8
1972	4,953	2,949	375	560	229	684	8	12	17	7
1971	6,053	2,753	389	517	214	563	11	11	13	7
1970	3,335	1,497	320	499	216	510	9	11	8	5
1969	2,706	1,245	192	236	322	673	12	12	18	10
1968	4,229	1,540	188	204	256	499	10	8	13	5
1967	3,648	1,263	223	230	294	476	12	9	22	5
1966	4,258	1,404	228	215	346	483	9	6	13	4
1965	7,331	2,014	226	177	351	471	3	2	7	2
1964	4,094	1,222	227	185	380	493	4	3	16	6
1963	3,675	1,090	175	153	430	502	7	5	27	8
1962	4,272	1,174	180	143	554	598	8	4	6	2

Table 2.--Weight and value of tuna catch of night handline fishery.

	Weight (MT)			Value (thousands of US$)		
	1973	1974	1975	1973	1974	1975
Bigeye tuna	65.4	120.2	63.1	102.6	249.8	149.5
Yellowfin tuna	23.3	22.9	75.5	38.0	38.4	157.0
Albacore	0.4	0.2	16.1	0.5	0.2	21.0
All tunas	89.1	143.2	154.6	141.1	288.2	327.5

Table 3.--Methods of chilling used by handline fishers in Hilo, Hawaii.

Method A - crush ice (not mixed with water)
random cuts for bleeding (few, often none)
5 min on deck between catching and chilling

Method B - 600 lb block ice mixed with seawater
at least two cuts for bleeding
5 min on deck between catching and chilling

Method C - 600 lb block ice mixed with seawater
at least two cuts for bleeding
longer than 5 min on deck

Method D - 300-450 lb of ice mixed with seawater
no cuts for bleeding
5 min on deck between catching and chilling

Method E - 300-600 lb of ice mixed with seawater
random cuts for bleeding
45 min truck ride (without ice) to auction market.

Table 4.--Fish body temperatures (°C) at time of auction.

Method	Number of fish	Average superficial temperature	Average deep temperature
A	17	14.9 ± 0.59	22.74 ± 1.68
B	44	15.26 ± 0.61	24.05 ± 0.77
C	14	17.20 ± 0.90	21.21 ± 1.43
D	21	19.50 ± 0.77	26.61 ± 0.75
E	6	19.80 ± 0.51	24.50 ± 1.82

Table 5.--Comparison of body temperatures by method of chilling (analysis of variance tests).

	Superficial temperature					Deep body temperature			
	B	C	D	E		B	C	D	E
A	0.49	2.30*	4.60**	4.85**	A	1.31	1.53	3.87*	1.76
B		1.94	4.24**	4.49**	B		2.84	2.56	0.45
C			2.30	2.55**	C			5.40**	3.34
D				0.25	D				2.11

* = significant at the 0.05% level

** = significant at the 0.01% level

Table 6.--Body temperature of burnt and normal tuna at time of auction (20 September-15 October 1977).

	Burnt	Not burnt
Sample size	11	18
Body temperature (°C)		
Deep	25.45 ± 3.03	25.01 ± 3.02
Superficial	17.40 ± 2.13	18.10 ± 4.11
Average fish weight (lb)	184.64 ± 35.88	197.94 ± 79.40
Sex ratio	6 males : 3 females	16 males : 1 female

Table 7.--The pH of tuna sampled at the Honolulu auction.

	All auction samples		Tail		Deep	
	Burnt	Good	Burnt	Good	Burnt	Good
N	17	5	6	1	4	2
$\bar{x}$	5.78	6.12	5.8	6.1	5.76	6.2

II. PERSPECTIVES: THE PAST, PRESENT, AND FUTURE OF TUNA PHYSIOLOGY

Andrew E. Dizon

Gary D. Sharp

A. *Introduction*

The workshop from which this collection of papers arose was intended to provide a forum for review of the various current studies on the physiological ecology of tunas and their near relatives; the review should lead to efficient consolidation of research efforts over the next several years. In addition, we hope that publication of these proceedings will encourage other investigators to lend their own particular expertise in this area. We feel that studies on the physiology and behavior of tunas have tremendous potential for the scientist concerned with fundamental principles (consider the extreme degree of specializations by tunas for efficient use of energy) as well as for the applied scientist (consider the commercial value of the tuna harvest). Because we want this volume to be of interest and use to more than the very few of us working in the field, we present in this section a brief historical review of tuna physiology investigations not covered in the preceding chapters. We will also include a short description of research in progress at the time of printing and conclude with our view of future potentially fruitful areas of investigation.

B. *The Captive Tuna*

The majority of what is known about the physiology of tuna has been elucidated through experiments carried out on live-held specimens at the Kewalo Research Facility of the National Marine Fisheries Service. It is presently the only facility in the world designed to maintain tunas in captivity for research purposes. Although it is difficult and expensive to maintain tunas in captivity, it is less so than carrying out observations of free-ranging tunas in the open ocean. In addition to providing fundamental data on how tuna function, the experiments on live-held tuna have delineated specific experiments that are best carried out on free-ranging tunas and have provided data for predictions regarding the distribution of tunas.

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The Kewalo Research Facility had its genesis in a contract awarded by the Pacific Oceanic Fishery Investigations (POFI) to Dr. Albert L. Tester of the University of Hawaii to do a literature search on the reaction of tuna to environmental stimuli (light, sound, chemicals, electric fields, etc.), to develop capture and holding procedures, and study the reaction of tunas to the above listed stimuli. Holding pens and tanks were constructed in 1951 at the Hawaii Institute of Marine Biology at Coconut Island, Kaneohe, Hawaii, and work commenced. The literature search was easy; there was no previous work. Fish were captured by trolling methods and returned for study. No skipjack tuna were returned alive, although they were often captured. Dr. Tester was successful at maintaining a few small kawakawa and several larger (up to 60 cm) yellowfin tuna (Tester, 1952). Experiments were designed to investigate sensory responses that might be exploitable with artificial bait. A well-developed chemical sense was established; tests of other sensory systems were not promising (Hsiao, 1952; van Weel, 1952). In the following year a second contract was awarded and the work continued on responses to chemical stimuli and to combined chemical and visual stimuli. Results revealed that amino acid fractions were the most excitatory and that colored lures had less attractive power than white ones (Hsiao and Tester, 1955; Tester, van Weel, and Naughton, 1955).

In 1956 POFI was incorporated into the new Bureau of Commercial Fisheries (BCF), and in 1957 a tuna behavior program was added to the organizational structure of the Honolulu Laboratory. Initial efforts were devoted almost exclusively to observing behavior of feeding skipjack tuna at sea. The Kewalo Research Facility was subsequently built in 1958 on 39,000 sq. ft. of land leased from the State of Hawaii; it was to serve jointly as the dock facility of the fishery vessels deployed by the BCF Lab and as the first aquarium facility devoted to the maintenance of live tunas for experimental purposes.

In 1961, John Magnuson, a fresh Ph.D. from the University of Minnesota, took command of the behavior program. Shortly after John arrived, he sailed on a 90-day cruise to the Line, Marquesas, and Society Islands on the *Charles H. Gilbert* (recently outfitted with underwater viewing ports). The mission: the comparative study of feeding behavior of skipjack and yellowfin tunas. As a result of his ocean-going experience, John returned convinced that too much research time was wasted while at sea and initiated a vigorous shoreside program of sensory and feeding studies.

Since Tester's early work at Coconut Island, Eugene Nakamura and his co-workers have been responsible for many improvements in both handling and holding techniques (Nakamura, 1960, 1962, 1964b, 1966, 1972; Magnuson, 1965). Two developments have contributed much to insure survival of returned tuna: (a) development of fiberglass transfer tanks with adequate amounts of supplied water and structured nonturbulent current flow (Nakamura, 1966) and (b) airstones constructed of grinding wheels that produce an oxygen stream of very fine bubbles allowing supersaturated levels of dissolved oxygen (Baldwin, 1970). These devices and an effort to insure that the captive tuna did not contact hard or abrasive surfaces made it possible to capture and deposit at the Kewalo Research Facility over a hundred 45-cm skipjack tuna with no mortalities.

Paralleling development of handling procedures were studies of sensory physiology. Investigations of behavioral responses to visual stimuli have spanned many years (Hsiao, 1952; Hsiao and Tester, 1955; Nakamura, 1968; Nakamura, 1969; Tamura, Hanyu, and Niwa, 1972; Hanyu, Tamura, and Niwa, 1973). Chemical sensing capabilities have also been studied extensively (van Weel, 1952; Tester, Yuen, and Takata, 1954; Tester, van Weel, and Naughton, 1955; Atema, Holland, and Ikehara, ms). Auditory responses of captive tunas were investigated by Iversen (1967, 1969).

Studies of behavioral facets of tuna feeding, swimming, and communication (reviewed by Nakamura, 1972) have been important to the conceptualization of the complex behavior and capabilities tunas exhibit. (In this volume, Kitchell *et al.*; Dizon, Brill, and Yuen; and Magnuson have reviewed previous studies of feeding, respiration, and hydrodynamics of tunas.) Matsumoto and Skillman (ms) are attempting to document relevant fisheries' information from scientific and fishery studies of Pacific skipjack tuna.

C. *The Warm-bodied Tuna*

The observation that tunas are warm has preoccupied most of the recent investigators in tuna physiology, and indeed most of the studies dealing with tunas (hydrodynamics, feeding, and energetics) have been undertaken to ascertain the reasons for warm-bodiedness (for detailed review, see Chapter 4, The Thermal Biology of Tunas). Yet, the fact that they are unequivocably warm has only been established within the last 20 years and the adaptive value of warmness, while being the subject of intense speculation, has yet to be established.

Although no evidence of thermoregulation arose from the studies of skipjack tuna at Kewalo Basin during the early 1970's, it was established that skipjack tuna can be very hot, relatively speaking, and that swimming activity seemed constant in the face of decreasing ambient temperatures. A Q_{10} of 1.0 was observed for swim speed of skipjack tuna, and this could be construed as support for a constant internal temperature.

The researchers working at Kewalo Basin were primarily interested in determining factors that would provide insight into the adaptive advantage of being warm (Neill *et al.*, 1976) and focused on the ability of tuna to detect temperature and temperature change (Dizon *et al.*, 1974, 1976; Steffel *et al.*, 1976) as well as the curious temperature compensation of swimming speed in skipjack tuna (Dizon *et al.*, 1977). Yet, no evidence of short-term physiological thermoregulation was obtained; in fact, the interpretation of thermoregulation by the ultrasonic transmitter-carrying giant bluefin tuna was questioned (Neill and Stevens, 1974). Because of the large mass and retarded thermal exchange of tunas, once warm they tend to stay warm, at least over periods of hours. Tunas have significant thermal inertia; using equations developed for quantifying this inertia, Neill and Stevens were able to account for the constant body temperature of Carey's giant bluefin tuna on the basis of thermal inertia. A dewar flask with an internal heat source could have done just as well. Unfortunately, the bluefin tuna carrying the ultrasonic transmitting gear did not stay in the cold water long enough to establish active physiological thermoregulation. Even now the question is unanswered, but it appears that completion of a few relatively simple experiments given present facilities will confirm that at least rudimentary thermoregulation exists, even in the small tunas.

D. Recent Projects

Behavioral and physiological experiments of great sophistication are now possible at the Kewalo Research Facility. Techniques have been developed that allow at least some limited experimental manipulation of captive animals. Laboratory telemetry devices have been developed that allow continuous monitoring of deep body temperatures (see Dizon, Brill, and Yuen, this volume), and recently of muscle activity. An active respirometer has been built and oxygen utilization at speeds above basal rates is being determined, since extrapolations of existing respiration data beyond 2 lengths sec^{-1} yield suspiciously high values. A swimming tunnel (aquatic treadmill) that allows control of swim speeds to about 4 lengths sec^{-1} is available which also allows tubes and wires to be positioned on a continuously swimming fish. Metabolic, heat flow, and electrophysiological studies are under way using the swimming tunnel. Work continues to collect stasis metabolic rate (respiration rates at zero overt activity). A promising study has been initiated to investigate the involvement of the adrenocorticosteroid hormones in causing stress-related mortalities in our captive fish. Use of corticosteroid blocking drugs may prove to be an effective remedy.

The studies of the biochemists continue (Guppy; Guppy, Hulbert, and Hochachka, this volume) with the intention of obtaining data from tunas performing specific activities above minimum hydrostatic swim speeds. Recently initiated studies of behavioral responses to water turbidity have not yet yielded sufficient results to warrant discussion.

Elsewhere in the world, Inoue and co-workers are continuing to study larval tuna development with an eye toward culturing tunas for the Japanese markets (Inoue, 1973). In La Jolla, the Southwest Fisheries Center maintains an active tuna oceanography program that has concentrated its efforts on the North Pacific albacore. Within this program there are continuing efforts to develop a "life-support" system to return live albacore to shoreside facilities.

To date, the Kewalo Research Facility in Hawaii remains the only site where captive tunas are routinely kept for experimental purposes. Skipjack tuna, kawakawa, and yellowfin tuna are available year round for study. Size ranges available are 30 to 70 cm for three tropical species. Efforts are continuing to make a larger size range available.

E. Future Research

The success of any ambitious program for physiological research on tunas requires a commitment to develop a routine and dependable system for capture, transportation, and maintenance of a variety of species of tunas; diverse temperature requirements of the tunas preclude a facility that would be capable of experimental work on both the temperate and tropical forms. Other favorably located facilities should be sought. The success of the Kewalo Research Facility of the Southwest Fisheries Center's Honolulu Laboratory is due in part to efforts of its personnel toward developing maintenance techniques. Fortuitous location of the laboratory (virtually next door to the tuna boat docks) and an active, interested, and cooperative fishery allows acquisition of specimens of tropical tunas with an absolute minimum amount of handling.

A full-scale "animal husbandry" approach would be ideal but possibly unrealistic, if only because of funding exigencies. We can, however, begin to lay the foundation for the transition from today's "maintenance-oriented" programs. Problems of transportation to the facility and experimental manipulation (even weighing is a risky undertaking for these delicate fish) would be vastly simplified by employment of a fast acting-fast recovering anesthetic. Two types are necessary: *(a)* oral delivery via food; and *(b)* injectable (intravenous injection is, however, virtually impossible). The study of stress and stress-related diseases is in order. Skipjack tuna develop "puffy-snout," a cluster of symptoms characterized by a lumpy, bumpy snout. Crowding or other types of stress causes development of the symptoms in less than 1 week. The study of hormones and hormone-blocking agents will, we hope, yield insights into causes and solution to this problem. So many other important and potentially manipulatable physiological properties of tunas are simply unknown; a program collecting baseline clinical data is needed. Considering the worldwide value of the tuna resource, we ought to know at least as much about the tunas' biological properties as we do about the salmonids.

Tunas have been kept alive for up to a year in the Kewalo Research Facility. If we can routinely accomplish this, especially on the puffy-snout-prone skipjack tuna, physiological studies requiring measurements on the same animal at different sizes become practical. Thus a great deal of sampling variability is eliminated. At present, the continuous flow of individual specimens almost insures that experiments are conducted on a mix of at least two different stocks (Sharp, this volume). As the ability to keep tunas improves, the potential for a breeding and rearing program becomes obvious. Domestication is not a goal, but at present individuals smaller than 30 cm or larger than 70 cm are unavailable for experimental study. The logistic problems of capturing and transporting large fish for study are almost insurmountable. Tank-bred stock might be a solution. Accessibility of larval and post-larval tunas would allow application of experimental strategies perfected by Reuben Lasker and his colleagues (Southwest Fisheries Center, La Jolla) to study fish year-class abundance questions. Whatever goals are eventually achieved, improvement in transportation, maintenance, and manipulation can only lead to more rigorous experimentation and more valuable information for interpretation of habitat-related behavior of high seas tunas.

Captive-fish studies must be supplemented by studies conducted in the field. We are currently planning experiments based on deployment of sonic tags on free-ranging tunas. A multisensor sonic tag can be developed using state-of-the-art electronics that will sequentially transmit information from a variety of sensors. Information from a practical four-function tag will generate real time information on ambient water temperature (surrounding the fish), depth of swimming, fish core temperature, and, most importantly, swimming activity. The latter information will be measured as tail beat rate. We propose that development of such tags be cooperative so that redundant costs will be minimized. As long as tags remain small enough to be deployed on 70 cm fish, one tag design should be adequate for all species.

Among the experiments which can be directly applied to practical problems of fishery management are studies of school cohesiveness. Tagging of several fish (requiring either heroic endurance of the tracking personnel or well-engineered equipment) would very rapidly yield information of school cohesiveness as a function of stock, fish size, and species. Present-day fishery strategies are predominantly two-dimensional and surface-oriented where fish are vulnerable only when they appear at the surface (longline fisheries are an exception); depth telemetering capabilities provide the necessary third dimension to location. Tagging a tuna with a high-output sonic tag and following it may prove to be an effective method of locating fish which spend only a small proportion of time at the surface. Tags and tracking gear are inexpensive and simple to operate relative to the cost in time and fuel resources that go into scouting for fish schools. Certainly, tuna are much more adept at finding conspecifics than fishermen are at finding their prey; a "Judas" fish location strategy may well be very cost effective.

Simultaneous collection of ambient temperature, core temperature, and activity parameters are necessary to elucidate the mechanics and strategies of tuna thermoregulation. These three parameters segregated and studied by fish size, stock, and species provide the basic, and probably most likely, data set that will clarify the adaptive advantages of thermoregulation, resolve stock and species differences, and perhaps, most importantly, allow development of an accurate energy budget for the various species and stocks. The latter is imperative for any future development of biomass models. For a tuna, the greatest energy cost is swimming; yet we have only the most rudimentary estimates of daily activity patterns. As Sharp (this volume) suggests, activity (and the respiration that quantifies its cost) is the ultimate character upon which natural selection operates to segregate stocks and species. Knowledge of activity patterns will always be the sine qua non of any live tuna studies, and tracking of free-swimming fish is the most cost effective manner in which to collect realistic information.

Considering the vast amount of material to be gathered and the unanswered questions, it seems likely that it will be a while before the total description of the various tunas' habitats will be made. It should be apparent, however, that existing information can be integrated into present-day fisheries strategies to provide for more efficient and effective exploitation of the tuna resources. The process of getting the knowns implemented into the fishing communities has its own set of problems, and increasing the knowledge about tunas has others. It takes intense dedication to get either job done. We hope that this volume will be a start and help to provide conceptual guidelines for researchers, administrators, the fishing communities, and other interested individuals, so that some day it will be possible to say that we truly "understand" the tunas and be able to apply that understanding to the benefit of both men and tunas.

7809

III. CORRELATIONS BETWEEN ENVIRONMENT, PHYSIOLOGY, AND ACTIVITY AND THE EFFECTS ON THERMOREGULATION IN SKIPJACK TUNA

Andrew E. Dizon

Richard W. Brill

Heeny S. H. Yuen

A. *Introduction*

Anyone who is familiar with live tunas must surely be impressed with the tremendous morphological investment in adaptations for high speed swimming. And anyone who is conversant with engineering principles must be aware of the extra energy required for even small increases in swim speed. Because of these high costs involved in the evolution and maintenance of a high velocity life style, the ability to swim rapidly must be critical to survival and success of the family in terms of range as well as numbers. Thus, an understanding of the tunas' performance, responses, and physiological mechanisms of swimming should illuminate their habitat requirements. This is essential for efficient management of this valuable resource.

In the main, behavior for a tuna consists of going fast at some times and slow at others. Every aspect of the tunas' behavioral repertoire should have a characteristic optimized velocity associated with it. Food search, feeding, and migration must be tuned for optimum efficiency to enable survival in the patchy and unproductive areas that are characteristic of the tuna environment. It is possible through direct experimentation, hypothesizing with mechanistic models, and through correlation studies in conjunction with fishery oceanographers, to come to an understanding of the interrelation between environment, activity behavior, and physiology of the tuna.

Four recent experimental models form the framework for much of our recent work at the Tuna Research Facility at Kewalo Basin. Two models, one mostly empirical and the other mostly theoretical, can be used to predict core temperature, given water temperature and velocity. The third deals with aspects of growth and energy requirements and their interrelation with activity levels. The last model uses physiological data from experimentation on captive fish and maps a hypothet-

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ical habitat in the central Pacific Ocean; in doing so, some peculiar aspects of skipjack tuna distribution are clarified.

We will first briefly summarize the models' important features and then describe the body temperature models in greater mathematical detail later in this report.

The "empirical" model has its genesis in the work of Neill, Chang, and Dizon (1976) in which rates of core temperature change were measured in restrained fish subjected to abrupt ambient temperature shifts. Rates at which new equilibrium temperatures were achieved were measured and appropriate constants determined. These constants were tissue- and weight-specific, and they describe rates of temperature change as a function of an integrated driving gradient; that is, the difference between actual body temperature and equilibrium temperature. Equilibrium temperature is defined as that body temperature achieved after thermal equilibrium is reached, always a positive value with respect to the ambient. The coefficient of temperature change is thus a measure of thermal inertia. Equilibrium body temperature is that temperature at which the rate of temperature decrease estimated by the coefficient of temperature change is equal to the rate of temperature increase of that point in the tissue warmed by metabolic processes. The amount of energy liberated during swimming can be estimated from respiration studies on free-swimming fish. Oxygen consumption can be converted to caloric values and point respiration values assumed (more about that later). Heat production can be translated to temperature terms using the heat capacity of muscle. Thus, respiration rate of a whole fish is a function of swim speed and, via machinations to be described, a determiner of rate of temperature increase of a point of tissue within the core of the animal.

The weakness of this approach is the coefficient of temperature change; we have no theoretical reason to assume that it stays constant under conditions of varying activity. (However, experimental results would indicate that it might.) The model formulated by Sharp and Vlymen (this volume) circumvents the problem by considering whole body rates of heat loss. The relationship of thermogenesis to metabolism and swimming energetics was developed to estimate heat production rates, and subsequently a heat dissipation model was formulated for a generalized tuna form, and with estimated heat production rates, used to predict core temperature at specific activity and size levels.

Kitchell, Neill, Dizon, and Magnuson (this volume) use fish bioenergetic principles and respiration and feeding data collected at Kewalo Basin to develop a comprehensive spectrum of energy needs as a function of body weight for various life processes. Results indicate that growth in small (less than

7 kg) skipjack tuna is limited by food consumption rates, whereas growth in larger fish is curtailed by physiological constraints on activity and metabolic demand. However, we know nearly nothing about distribution of activity of wild fish in nature. We are confident that an energetic cost could be placed on various levels of activity, but more work must be done to measure actual distribution of swim speeds in real fish as a function of size. In this report we will present estimates of activity distributions.

Perhaps the reason for live studies, at least in terms of fishery science, is exemplified in the hypothetical habitat model of Barkley, Neill, and Gooding (ms). Using laboratory findings on temperature and oxygen requirements of skipjack tuna, these authors explain why large tuna are probably excluded from regions of the eastern tropical Pacific Ocean and that while skipjack tuna in the tropics are known to be abundant they are seldom observed. Because of size-related and activity-related upper temperature limits and a restrictive oxygen tolerance, larger-sized fish cannot find areas that are sufficiently cool and still have adequate amounts of dissolved oxygen. Their work also suggests that the habitat of adult skipjack tuna is the upper thermocline and not the mixed layer. Our report will deal with the ability of skipjack tuna to maintain activity at various temperatures.

We have organized this presentation into three broad topics; data from the various experiments will overlap the topics. The first will deal with "real world" estimations of tuna performance based on data from free-swimming fish carrying depth-sensitive ultrasonic transmitters. These data also provide some idea of the limits of preferred habitat within those available to the fish in the tracking area. The second topic is organized from those experiments relating behavioral responses to alterations of the environment. Experiments will be described relating skipjack tuna responses to variations in light, salinity, oxygen, and temperature. In some cases, data on the responses of yellowfin tuna will be drawn upon for comparison. The third topic is the interrelation of environment, behavior, and physiology. We will limit our discussion to water temperature and activity effects on core temperature. The efficiency of both models in predicting core temperature will be examined and the topic of thermoregulation in skipjack tuna discussed.

Before proceeding with the topic of tracking, we would like to put the concept of swimming speed into energetic terms. Throughout this report, we will be using specific swim speeds to report results. As Webb (1975) puts it, "specific swimming speeds remain the simplest and most useful method of comparison [p. 51]." However, performance-size effects are neglected and we have to remind ourselves continually of what changes in swim speed must really mean to the animal. If specific swim speed is scaled against size and energy consumption (Fig. 1), the high cost of fast swimming becomes apparent. A 50-cm skipjack tuna requires about 1 cal $\sec^{-1}$ to swim at its minimum hydrostatic equilibrium speed; at 10 lengths $\sec^{-1}$, 100 cal $\sec^{-1}$ are required (or 418 watts). And we have observed skipjack tuna swimming more than 20 lengths $\sec^{-1}$. In terms of heat dissipation and energy reserves, fast swimming is indeed costly.

B. Performance of Tracked Skipjack Tuna

The power required to propel an object through the water is related to its length, drag, and velocity; the relationship of these variables is known through much experimentation on animate and inanimate objects (see Webb, 1975, for review). However, notably lacking in the literature is data on real velocity levels partitioned on daily and maybe even lifetime intervals. This paucity of data is obviously due to the difficulty in experimental implementation in wild fish. Although we

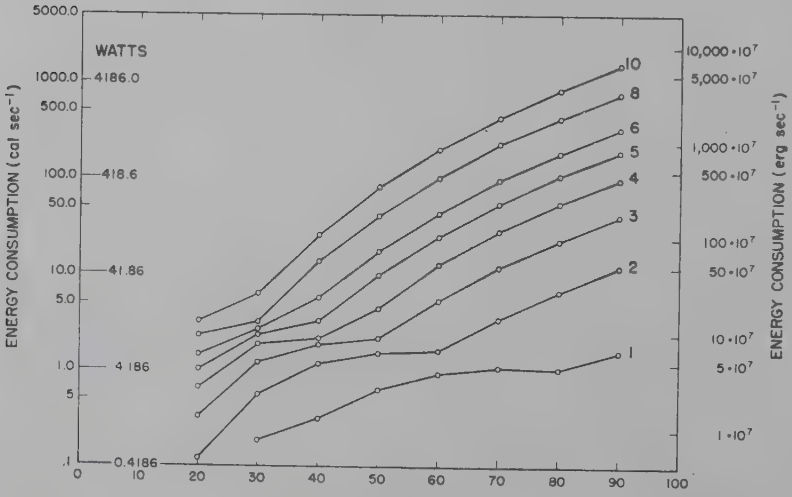

FIG. 1. Specific swimming speed (lengths $\sec^{-1}$) is translated into energy consumption terms as a function of fish size. Swimming speed/power relationships are from Sharp and Francis (1976).

know approximately what energetic costs might accrue for a hypothetical distribution of activities, we need data on real activity levels.

Equipping wild (freely ranging) fish with ultrasonic transmitters and following their movements in the ocean over several days is the most practical method so far developed; presently it has serious shortcomings. Resolution of small-scale movements is poor. These movements might contribute strongly to the total energy consumption. Effects of the transmitter on drag coefficients and of handling on behavior could be a problem. Long-term collection is impractical because of ship costs and lack of endurance of personnel. Nevertheless, tracking has provided first-cut estimates of performance, preferences, and activities and is worthwhile for such purposes.

Six skipjack tuna have been tracked to date; Yuen (1970) tracked two small "bank" fish (approximately 45 cm) in the late 1960's. Behavior of these fish was remarkable; days were spent on the banks, nights off the bank. Distribution of estimated swimming speeds was strongly weighted toward speeds below hydrostatic minimums, implying that small-scale movements were very important. No data on temperature or depth could be collected.

In May of 1977 we tracked three larger "season" fish (approximately 70 cm) and in October tracked another small (approximately 45 cm) bank fish. Behavior of the small fish was virtually identical to that of Yuen's fishes. Behavior of the larger fish, however, seemed independent of the banks, and data collection was improved using depth-telemetering tags.

Skipjack tuna were tagged by a technician aboard a commercial pole-and-line vessel. During scouting operations prior to fishing the RV *Townsend Cromwell* (the tracking vessel) shadowed the fishing boat in readiness. Tags employed were cylindrical (16 mm dia. by 92 mm long) and transmitted on a frequency of 48 khz. Pulse rates were determined by depth and varied from 60 at the surface to about 150 at 300 m. The tags had a useful life of approximately 3 days and a range of less than 2 km.

Five season fish were actually tagged on separate occasions; tags were force fed to the tunas. Two of the five regurgitated their tags before any useful information was obtained; one immediately after release, the other after 2 h. The remaining three were tracked for 24, 11, and 10 h (Table I). We had visual confirmation that at least two of the fish rejoined their schools after release; we sighted large skipjack tuna schools at the range and bearing of our tagged fish. Relative to small tuna tracked previously, these larger tunas proved difficult to track since their occasional bursts of speed moved them rapidly out of tracking range and

TABLE I. Summary of Ultrasonic Tracking Data

	Fish (skipjack tuna, 70 cm FL)		
	A	B	C
Time tagged (l.s.t.)	1230	1030	1600
Tracking period (h)	24	11	10
Termination	lost	lost	died
Total distance swum (km)	141.6	50.2	24.8
Mean velocity (m sec^{-1})	1.64	1.27	0.72
Mezn velocity (lengths sec^{-1})	2.30	1.75	1.03
Mean depth (m)	68.6	143.1	231.7
Mean temperature (°C)	22.4	20.1	14.9

were responsible for the eventual termination of two of the tracks. The third fish apparently died since he began to slowly sink into very cold water about 10 h after tagging. The sinking rate was too slow to indicate a free-falling regurgitated tag and we had the impression of a gradually weakening tuna maintaining positional equilibrium but swimming too slowly to maintain hydrostatic equilibrium (Magnuson, 1973). In about 30 min, the fish glided from 120 m to 450 m (7.5°C) when we terminated the track.

Since depth information was available, we were able to improve our estimates of swim speed by accounting for small-scale vertical movements. Behavior of our fish was characterized by many rapid vertical migrations superimposed on a fairly consistent northwesterly migration. Horizontal positions were determined every half hour; vertical positions, approximately every 3 min. Movement was then assumed to be from depth position to depth position along the hypotenuse of a triangle whose horizontal leg was determined from half-hour position information. The vertical leg was determined by the difference in two adjacent depth measurements. Thus, our swimming speed estimates are better than those obtained with only the horizontal component of velocity but are still underestimates of what the fish was actually doing. The estimates were most accurate during periods of relatively fast horizontal movement on a steady course. During periods when the fish was feeding and circling, our estimates fell below the minimum hydrostatic equilibrium speed.

Skipjack tuna A, tracked for 24 h, traveled 141.6 km horizontally and vertically (Table I). All three fish resolved about 10% of their total movement into vertical migrations. Mean velocities ranged from as high as 2.30 lengths sec^{-1} (164 cm sec^{-1}) to less than hydrostatic equilibrium speeds in the case of the fish that died. Mean depths and temperature varied considerably among the three fish (Table I). Skipjack tuna C's swimming depth is deeper, and the temperature encountered is colder than the others because of its gliding descent. If the glide is excluded from data set, mean depth is 87.8 m and temperature is 21.4°C, both of which are intermediate between Fish A and B.

All three fish remained in water above 20°C during 85% of the track periods although all fish did dive to cold water which would ultimately prove lethal if they remained indefinitely at these temperatures (Dizon, Neill, and Magnuson, 1977). Figure 2 is a frequency distribution of temperature observations; fish C only includes data prior to glide to depths. No thermocline was evident during the tracking periods (Fig. 3) so no observations of fish position relative to the thermocline can be made. (It is interesting to note that these fish do not violate activity-size boundaries hypothesized by Neill, Chang, and Dizon, 1976); fish of this size at activity levels equivalent

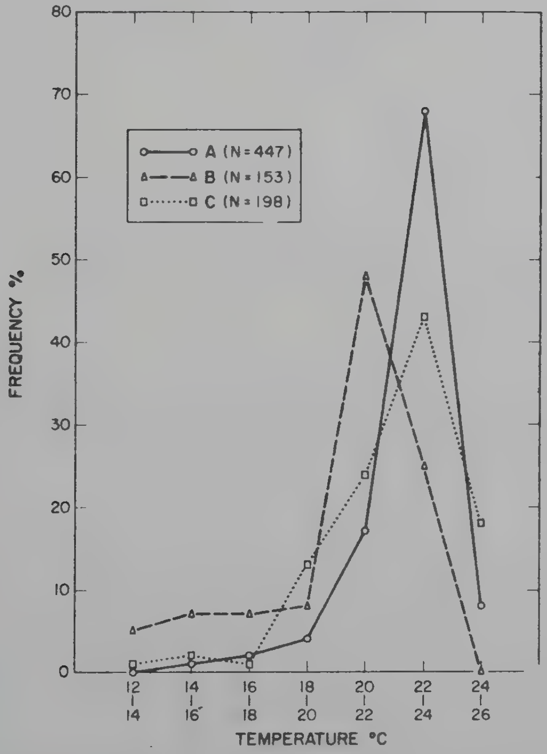

FIG. 2. Distribution of temperatures encountered by three fish tracked with ultrasonic transmitters.

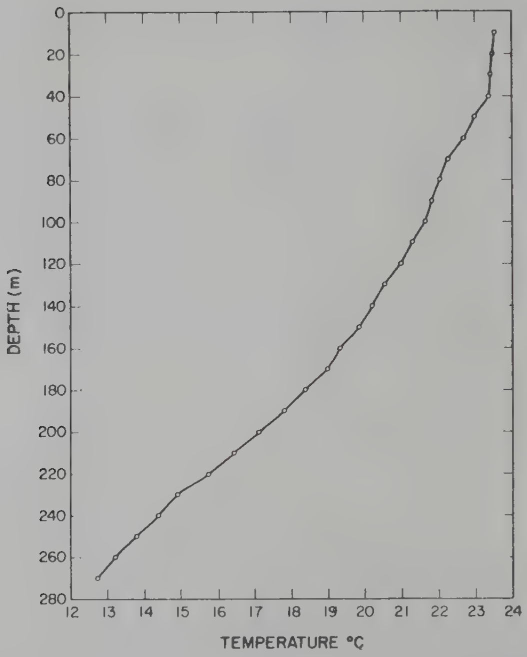

FIG. 3. Typical temperature profile occurring during tracking period.

to 3 mg O_2 $g^{-1}h^{-1}$--suggested as the average metabolic rate in red muscle of normally active tuna--must remain in water below 23.5°C. Water above this temperature was not available during the tracking period.)

Distribution of measured swim speeds varied considerably among the three fish (Table II). Speeds below minimum hydrostatic equilibrium speeds were observed; obviously small-scale movements were occurring during those sampling periods. As speed increases, the accuracy of our measurements did also since the fish was more likely to swim a straight course. Fish A was the best performer and demonstrates remarkable abilities (Table III). The intervals in this table are continuous observations of swim speed without rest and seem to be periods when the fish was moving rapidly, perhaps from one feeding area to another. The high velocities and relatively warm temperatures indicate to us that the fish must have some mechanism to rid themselves of the terrific amount of heat generated; at the highest velocity (6 lengths sec^{-1}) approxi-

TABLE II. Distribution of Swim Speeds (Sampled at 30-Min Intervals)[a]

	Fish (skipjack tuna, 70 cm FL)		
	A	B	C
Below 1.33 (lengths sec^{-1})	27	45	58
1.34 to 2.33	29	41	37
2.34 to 3.33	21	0	5
3.34 to 4.33	15	14	0
Above 4.34	8	0	0
Number of observations	48	22	19

[a] *Minimum hydrostatic equilibrium speeds for fish of this size is 1.33 lengths sec^{-1} (Magnuson, 1973).*

TABLE III. Maximum Swim Speeds Achieved by Skipjack Tuna A (70 cm FL)[a]

Interval (min)	Swim speed		Depth (m)			Temperature at depth (°C)		
	Lengths sec^{-1}	m sec^{-1}	Min.	Med.	Max.	At min.	At med.	At max.
30	6.08	4.33	6	53	85	23.5	22.9	21.9
60	4.89	3.48	2	6	38	23.5	23.5	23.4
120	3.85	2.74	2	15	56	23.5	23.5	22.8
240	3.10	2.21	54	143	262	22.9	20.1	13.1

[a] *Speeds are continuous for periods indicated with no resting periods intervening.*

mately 100 cal sec^{-1} are being consumed. (We will discuss this more in a later section dealing with thermoregulation.)

C. *Responses of Tunas to Environmental Parameters*

Before introducing the topic of thermoregulation, we would like to describe briefly some recent work with captive tunas responding to artificial environments. Our methods are simple; captive tunas were acclimated to a tank situation, their activity measured, and then some environmental parameter changed (oxygen, temperature, or salinity). Significant alterations in swim speed or swimming direction constituted a response. We observed two types of responses: "automatic" and "behavioral." Although there is no real evidence to support the distinction, it seems appropriate at least for the moment. Automatic responses were characterized by a gradual change in swim speed which follows the changing treatment level; a characteristic Q_{10} can be applied. Behavioral responses, in contrast, seem to be triggered responses and occur rather abruptly, presumably when a tolerance level or sensory level was reached. Of course, we did also observe intermediate-type responses.

For most of the work we have been using a tank system in which swim speed, direction, and temperature are automatically collected (Fig. 4). The swimming channel is equipped with photocells to record movement and has reasonably restricted dimensions (0.75 by 0.75 m) so that environmental changes can be made rapidly and economically. Intakes and discharges into the tank are made through countercurrent pipe systems so that spatial gradients are eliminated. The system will accommodate oxygen, salinity, or temperature changes.

Tuna--skipjack or yellowfin--did not seem to make any responses to salinity changes; when salinity was reduced from normal concentrations to below $20^{o}/_{oo}$, no alterations in swim speed were observed (Dizon, 1977, Table IV). Although our sample size was small, we are confident small salinity changes (of a magnitude that a tuna would experience) are not very important behavioral regulators.

Oxygen, in contrast, produces dramatic behavioral changes in skipjack tuna (Dizon, 1977). Skipjack tuna responded by increasing their swim speed abruptly when dissolved oxygen levels were reduced from saturated to 4 ppm; yellowfin tuna made no responses to 2 ppm, which was the lowest attainable in the system (Fig. 5). Eight skipjack tuna and three yellowfin tuna were tested; median swim speed changed from 1.6 lengths sec^{-1} at above 4.5 ppm to 2.0 lengths sec^{-1} at 3.5 ppm and 2.3 lengths sec^{-1} at 2.5 ppm (Fig. 6). These responses did not appear to be related to increasing ram jet ventilation because adequate oxygen could

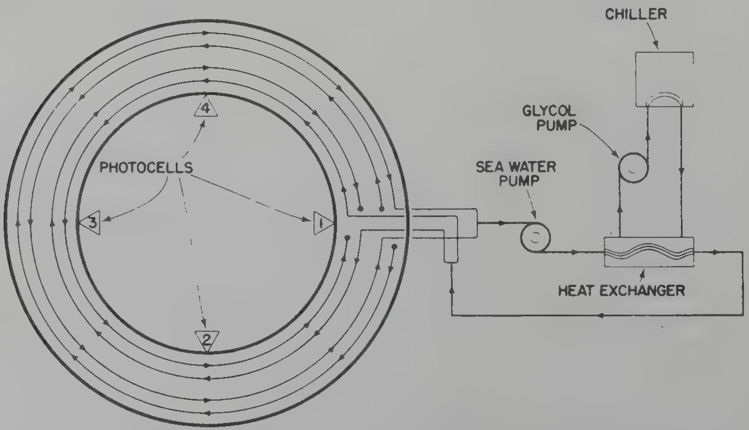

FIG. 4. Tank system for examining activity responses of tunas to spatial gradient-free alterations of oxygen, salinity, or temperature levels.

TABLE IV. *Effect of Decreasing Salinity on Swimming Speed in Tunas*

	n	$\overline{X}$	SD
Skipjack tuna			
Fish No. 1 (38.3 cm, 925 g)			
Before salinity change	28	2.10	0.40
During salinity change	22	1.82	0.40
Fish No. 2 (37.7 cm, 882 g)			
Before salinity change	44	2.03	0.26
During salinity change	12	2.37	0.19
Fish No. 3 (42.0 cm, 1.352 g)			
Before salinity change	30	1.21	0.07
During salinity change	15	1.16	0.06
Yellowfin tuna			
Fish No. 1 (45.3 cm, 1,491 g)			
Before salinity change	39	1.54	0.30
During salinity change	31	1.81	0.26

be had by increasing gape slightly. Increasing oxygen requirements of faster swimming offsets any increased ventilation. It did seem to be an appropriate behavioral response for a fish to remove itself from a suboptimal environment. However, in our tank it was maladaptive since no appropriate environment was available.

An example of the automatic response was the skipjack tuna's response to temperature. In this experiment fish were held for long periods of time at one of three treatment temperatures (20°, 25°, and 30°C). Swim speeds were measured for every lap over the 2- to 3-day experiment, 10 min averages were made and used for analysis. (Note that 6 laps equal 100 m swum.) Although reported earlier that temperature changes had no effects upon swim speed in skipjack tuna (Dizon *et al.*, 1977; Stevens and Fry, 1971) a slight effect was noted when extensive observations were made (Fig. 7). Yellowfin tuna, in contrast, had a swim speed/temperature Q_{10} equal to about 2 (Dizon *et al.*, 1977).

Behavioral type responses to temperature were also observed with captive fish. Some fish were noted to cease lap swimming when water cooled to 20°C and to initiate a characteristic reversal behavior consisting of swimming elongated figure eights extending about 4 m. We interpreted this behavior to be a response to stress, since it was observed at the low temperatures and also when a fish was initially introduced into the tank system.

If distance swum in 50 min is plotted against a time series of temperature, it is apparent that skipjack tuna were either exhibiting a stress response or were reluctant to swim

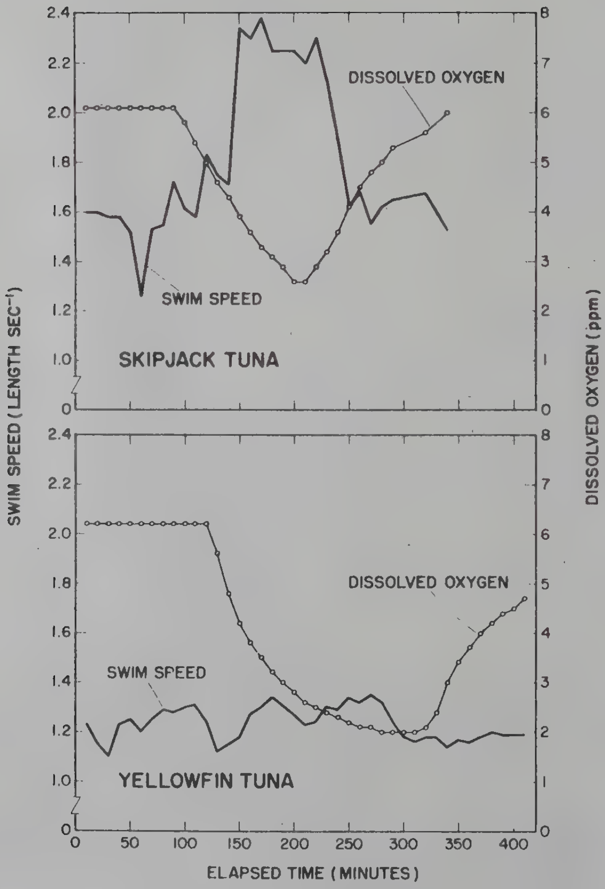

FIG. 5. Effect of dissolved oxygen level on swim speed in skipjack and yellowfin tunas. Swim speeds are median values sampled for 10 min periods (Dizon, 1977).

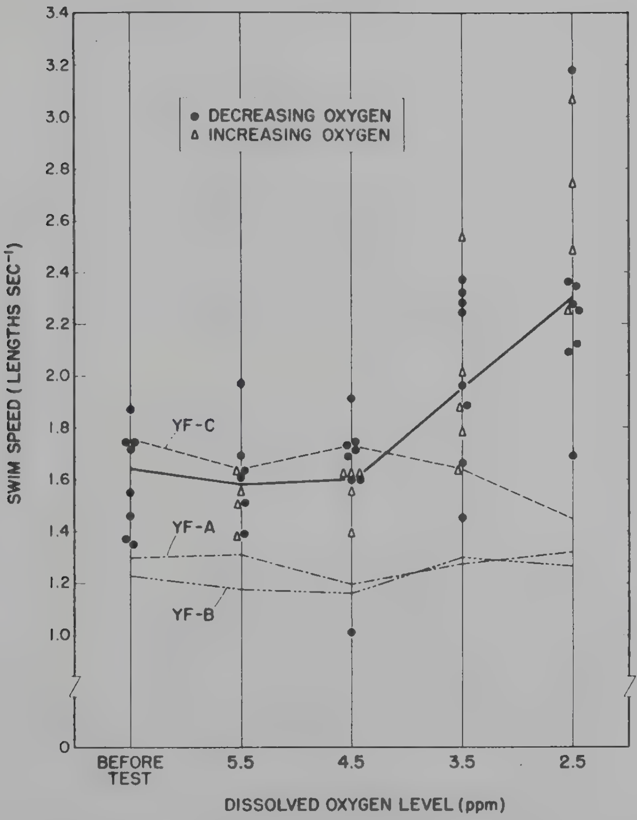

FIG. 6. Summary of data from responses of eight skipjack and yellowfin tunas. Solid dots--decreasing oxygen levels, median swim speeds grouped by 1 ppm intervals, and "before" test observations. Open triangles--increasing oxygen levels, median swim speeds grouped by 1 ppm intervals. Solid lines--grand median for skipjack tuna. Broken lines--individual medians for each of the three yellowfin tuna, decreasing oxygen levels only (Dizon et al., 1977).

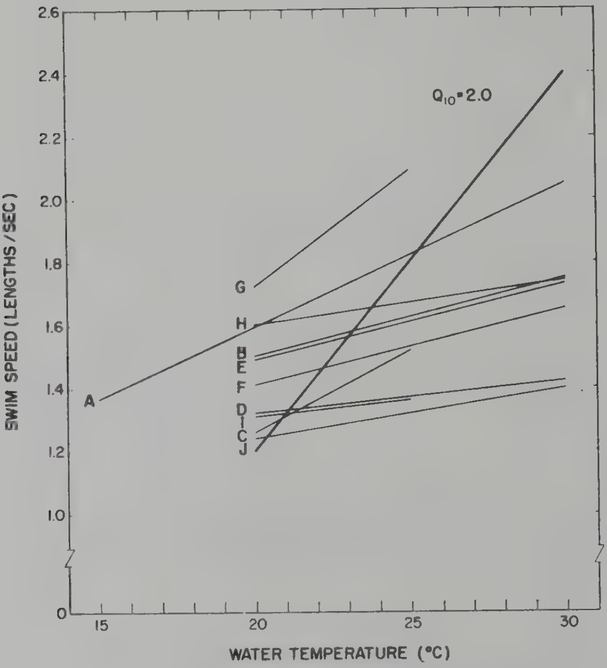

FIG. 7. Effect of temperature upon swim speed in 10 skipjack tuna. Lines fitted by linear regression analysis; all, save fish I, are significant at the 0.01 level. The median swim speed-temperature relationship of three yellowfin tuna (tested three times each) is also plotted, Q_{10} = 2.

any further into cold water (Fig. 8). Note how the response was not exhibited until many minutes of exposure to cold water. Body temperature had equilibrated long before responses were made. It was, however, difficult to quantify this behavior further since not all fish would respond in this manner (Table V). If the number of 10 min sample periods containing reversal are compared at 20°C and at 30°C, only two or three of the seven fish tested at 30°C respond. But we have repeatedly observed this response to cold water in other experiments and assume it manifests itself in wild fish in the reluctance of the sonic-tracked fish to spend more than an insignificant amount of time at temperatures lower than 20°C.

A curious response observed during the tracking study is

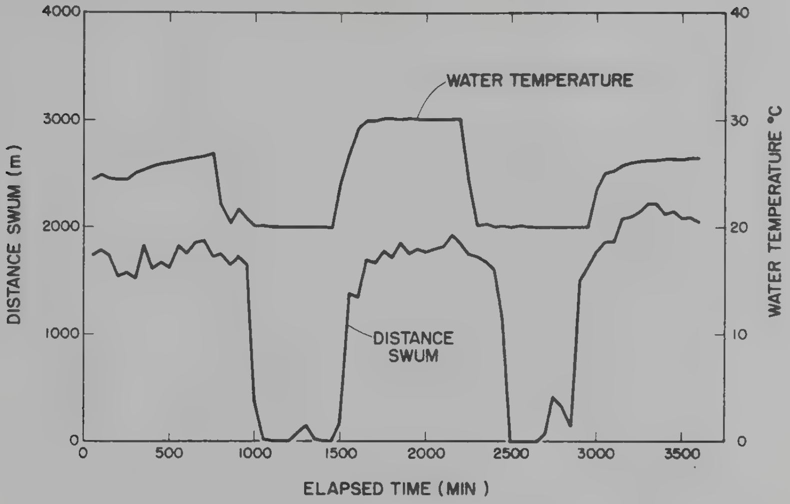

FIG. 8. Effect of temperature on willingness of a single skipjack tuna to swim laps in test tank. Distance swum is number of laps in 50 min multiplied by 16.67 (6 laps = 100 m swum).

TABLE V. Fraction of 10-Min Sample Periods That Contain Reversals

	Fish						
	A	B	D	E	F	H	J
20°C	0	.07	.78	.18	.60	.01	.05
30°C	0	.01	0	.02	.09	0	0

evident in Fig. 9; this fish ranged throughout the water column during the day. Time was spent at the surface and at depths as great as 263 m. However, at the end of twilight the fish rose into shallow water and remained there until dawn when an abrupt dive to 210 m was made. All three fish demonstrated evening ascents but data are missing for fish B and C for times comparable to the morning descent of fish A. Fish A swam at a mean depth of 58 m during the day, 14 m during the night; Fish B, 46 m versus 32 m; and Fish C, 70 m versus 19 m. We have no idea whether this was a response to food, light level, or some sort of endogenous rhythm. More work is planned in which we hope to examine these questions.

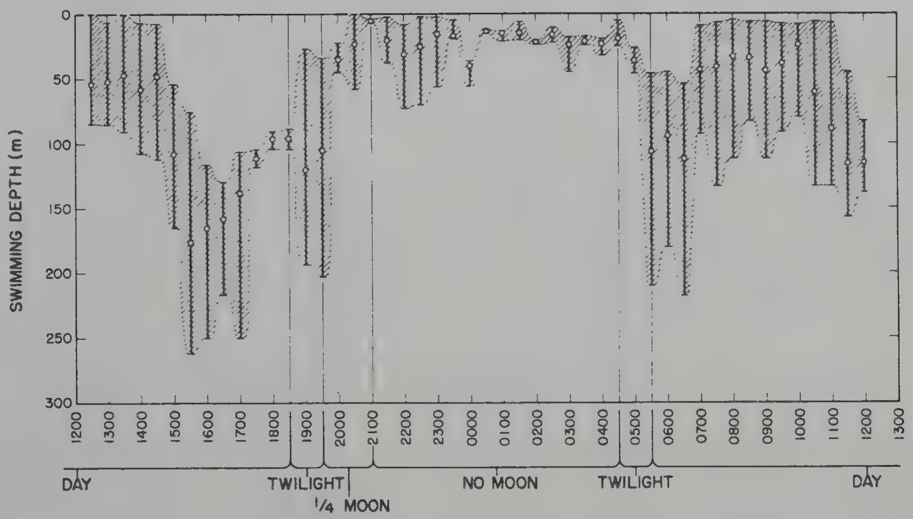

FIG. 9. Depth range (and median depths) plotted as a function of chronological time at 30 min intervals for skipjack tuna A. Depth measurements made on 3 min intervals.

D. *Activity and Water/Body Temperature*

Prediction of body temperature given swim speed and water temperature is very important for three reasons: (a) Predicting such a complex phenomenon usually means understanding it and statements can be made as to its importance. (b) Body temperature is a readily telemetered parameter whereas the related respiration rate is not; knowledge of daily respiration rates is essential to any growth and energy models. (c) Two circumstances occur in which high levels of activity are a problem. In areas of high water temperature activity might need to be curtailed to avoid excessive body temperature, and the fishes' efficiency at prey capture might be seriously reduced. Or during capture, frantic escape efforts might cause muscle damage and consequent reduction of market value--the so-called burnt tuna problem.

Interpretation of measurements of body temperature in wild fish suffer from unknown influences of past activity and temperature history. Most tracking work only measures location of fish and depth or temperature of the water. Accurate measures of activity, body temperature, and experimentally controlled environmental temperatures are necessary to formulate and test models predicting body temperature and to measure thermoregulating abilities in free-swimming tunas (Brill, Guernsey, and Stevens; Sharp and Vlymen, this volume).

As mentioned in the introduction, two approaches have been made to predict body temperature; the first is an empirical approach outlined in Neill and Stevens (1974) and Neill *et al.* (1976) and used to predict red muscle temperature in Dizon *et al.* (1977). Given the rate at which a tissue mass loses or gains heat (k) and the rate of heat production, the temperature of a tissue can be estimated as a function of any time series of temperatures encountered by the fish. From respiration studies by Gooding and Neill (ms), swim speed and fish weight were significant determiners of oxygen uptake:

$$\log r = -1.2012 + 0.2131\, s + 0.1911 \log w \qquad (1)$$

where

r = respiration rate, mg O_2 g^{-1} h^{-1};

s = swim speed, lengths sec^{-1};

w = fish weight, g.

Since the concern is red muscle temperature, we need an estimate of respiration rate of this tissue and for the moment we will estimate it to be about twice that of the whole fish on a per weight basis (Neill *et al.*, 1976). Thus

$r_{rm} = 2\ r$ and substituting into equation (1) (2)

$$\log r_{rm} = -0.9002 + 0.2131\ s + 0.1911 \log w \quad (3)$$

where

r_{rm} = red muscle respiration rate, mg $O_2\ g^{-1}\ h^{-1}$.

Respiration rate can be converted into an estimation of the rate of temperature change using the heat capacity of fish muscle (0.8 cal g^{-1} °C^{-1}) and the oxycaloric equivalent for fish (3.42 cal mg $O_2{}^{-1}$) (Neill *et al.*, 1976).

$$r'_{rm} = r_{rm}\ 3.42\ (0.8)^{-1}\ (60)^{-1} \quad (4)$$

where

r'_{rm} = red muscle respiration rate, °C min^{-1} and substituting into equation (3)

$$\log r'_{rm} = -2.0474 + 0.2131\ s + 0.1911 \log w. \quad (5)$$

Now, if the fish is in thermal equilibrium, body temperature is constant and heat production rate (r'_{rm}) must equal rate of heat loss. The tendency for the tissue temperature to increase must be balanced by temperature decrease through conduction and convection. Thus

$$r'_{rm} = k\ (T_{rm} - T_a) \quad (6)$$

where

k = coefficient of temperature change, °C min^{-1} °C^{-1};

T_{rm} = red muscle temperature, °C;

T_a = ambient water temperature, °C.

Excess temperature (T_x) is the difference between the temperature of the tissue and the water temperature

$T_x = T_{rm} - T_a$, substituting and rearranging equation (6)

$T_x = r'_{rm}\ k^{-1}$ which can be combined with equation (5) to give

$$T_x = \frac{10^{(-2.0474 + 0.2131\ s + 0.1911 \log w)}}{k} \quad (7)$$

The coefficient of temperature change (k) is dependent upon weight for the various tissues studied in skipjack tuna (Neill *et al.*, 1976):

$$k_{rm} = 0.044w^{-0.446} \quad (8)$$

where

k_{rm} = red muscle coefficient of temperature change, rate of temperature change per degree (°C) of driving gradient, °C min^{-1} $°\mathrm{C}^{-1}$.

Rather than approaching prediction of body temperature from the empirically derived functions of respiration and rate of temperature change, the theoretical model of Sharp and Francis (1976) and Sharp and Vlymen (this volume) has its beginnings in the power equation from hydrodynamic theory. In this equation, power, which can be converted to respiration terms, is a function of the coefficient of total drag, length squared, velocity cubed, and water density. Stasis respiration is added to respiration due to swimming, and the total is the caloric expenditure required for swimming at specific activity levels. The coefficient of total drag is obtained from literature values of Reynolds number (Re) which are functions of speed and organism size (Sharp and Francis, 1976); this value is assumed to approach a constant, 0.01, as Re approaches 6.8×10^{-5}.

Heat loss is based upon a forced convection model at the lateral surface of a tuna-sized cylinder. The entire metabolic surface is assumed to be located in this middle cylinder and conduction to the head and tail sections considered to be negligible. For a fish at equilibrium, heat loss (q_t) is again assumed to equal heat production (C_v) reduced by a muscle-propulsion efficiency term (M_e) so that

$$q_t = (1 - M_e)\ C_v. \qquad (9)$$

The relationship is then a complex function of the physical dimensions of the midsection cylinder, velocity, density of the fish and the medium, viscosity of the medium, thermal conductivity of the fish, heat capacity of the medium, metabolic mass of the fish, and magnitude of the driving gradient--T_x. The model also includes a term for the properties of heat lost via the gills (Q_g) which we have examined empirically.

Thus, two models are available that predict body temperature as a function of velocity and water temperature. Other values are available as accepted constants or are measurable parameters of the fish itself (length, weight, etc.). Problems, of course, occur in the estimation of total drag which is a sensitive parameter in determining T_x and stasis metabolic rate. The theoretical model thus requires some assumptions about drag, muscle efficiency, and stasis metabolic rate but is more soundly based than the empirical. Muscle efficiency terms are ignored in the empirical model, or are implied in the estimation of red muscle metabolism. Nevertheless both models form a starting point for the investigations of thermoregulatory performance in our captive fishes.

Activity under conditions of constant and variable temperatures was measured again in the ring tank system. Fish were equipped with ultrasonic transmitters with long probes that could be inserted into the muscle core (Fig. 10). Fish were captured from our outdoor tanks and placed in the channel for 4 h to allow recovery time from the effects of the capture and transport struggle. After that, the subject was persuaded to swim into a plastic bag and was removed from the channel. We held the fish by the jaw on an inclined plastic sheet; water was played over the gills, and the fish blinded with a dark rag over the eyes. The tag thermistor probe was inserted into the red muscle from the dorsal side just lateral of the forward edge of the dorsal fin. The tag body itself was secured to the corselet with two Floy dart tags or later with a Peterson-type button. The latter was faster and more secure. The procedure took less than a minute and the fish was then returned to the swimming channel.

The ultrasonic transmitter was developed at the Oak Ridge National Laboratory and generously loaned by Drs. Charles Coutant and James Rochelle. The tag was designed for telemetry of the body temperature of a small fish or the water temperature. The tag is 17 mm OD, 34 mm long, and weighs less than 14 g in water. Temperature is encoded by pulse interval modu-

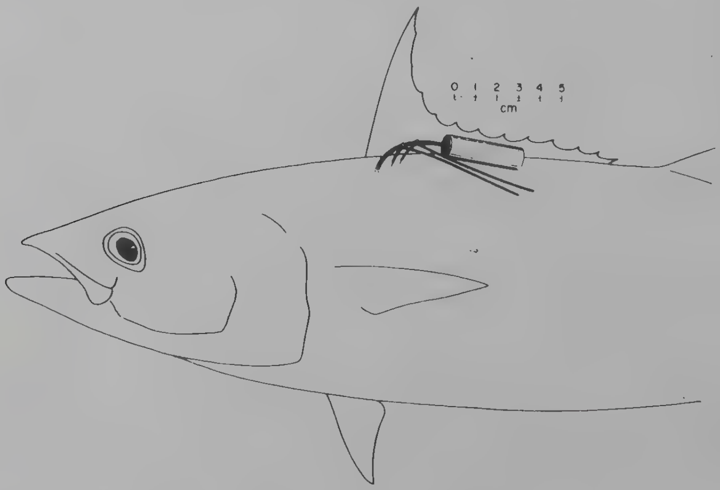

FIG. 10. Method of securing ultrasonic transmitter. Temperature sensitive element is located at distal end of the probe embedded in red muscle.

lation, with the interval varying from 1400 to 300 msec over a range from 5° to 35°C. This calibration shifts less than ±0.2°C throughout the expected life of 21 weeks and is not significantly affected by a thermistor-tag temperature differential (Rochelle and Coutant, 1974:1).

Test treatments consisted of 8 h treatments at three temperatures (4 h at 25°C, 12 h at 20°C, 12 h at 30°C, 12h at 20°C, and 8 h at 25°C and repeat). In one case 15°C was used, but it proved fatal and was discontinued. Body temperatures and activities were sampled at 10 min intervals for the former and were averaged at 10 min intervals for the latter. Swim speed was calculated for all laps swum during the course of the experiment. We attempted to test all ten fish at each of the three test temperatures; three fish did not survive the 20°C treatment.

Surprisingly, initial analysis of the results showed no correlation between swim speed and body temperature; as swim speed increased, body temperature sometimes decreased, sometimes increased, or sometimes stayed the same (Fig. 11). No pattern was evident in the ten fish and it was obvious that intercorrelations between swim speed, environmental temperatures, and body temperatures made any type of multiple regression analysis impossible.

Use of the two models and a smoothing function designed by Neill and Stevens (1974) proved effective in sorting out the interrelationships between the variables. The data set in turn provided a method of testing the effectiveness of the two models. But it was immediately clear from observations of the T_x's from the data that the theoretical model predicted body temperatures that were too high. From data collected by Brill, Guernsey, and Stevens (this volume), we learned that a significant amount of heat could be leaking from the central heat exchanger to be dissipated at the gills. Sharp and Vlymen (this volume) recognized the problem of fishes with central heat exchangers and suggested that one reduce the predicted body temperature by at least 50% to account for heat lost at the gills; but in most cases this is not enough.

The empirical model, in contrast, sometimes predicted too high and sometimes too low.

For comparison purposes it was decided to force each model to fit the mean T_x and the mean swim speed at 25°C before attempting to compare their effectiveness. We adjusted the amount of heat lost at the gills (heat exchanger effectiveness) to force the fit of the theoretical model. We adjusted the respiration multiplier (the degree to which muscle respiration exceeded whole fish respiration) to force the fit of the empirical model. The results are shown in Table VI. According to the theoretical model, skipjack tuna lose at the gills from 0.83 to 0.53 of the heat generated by muscle contraction,

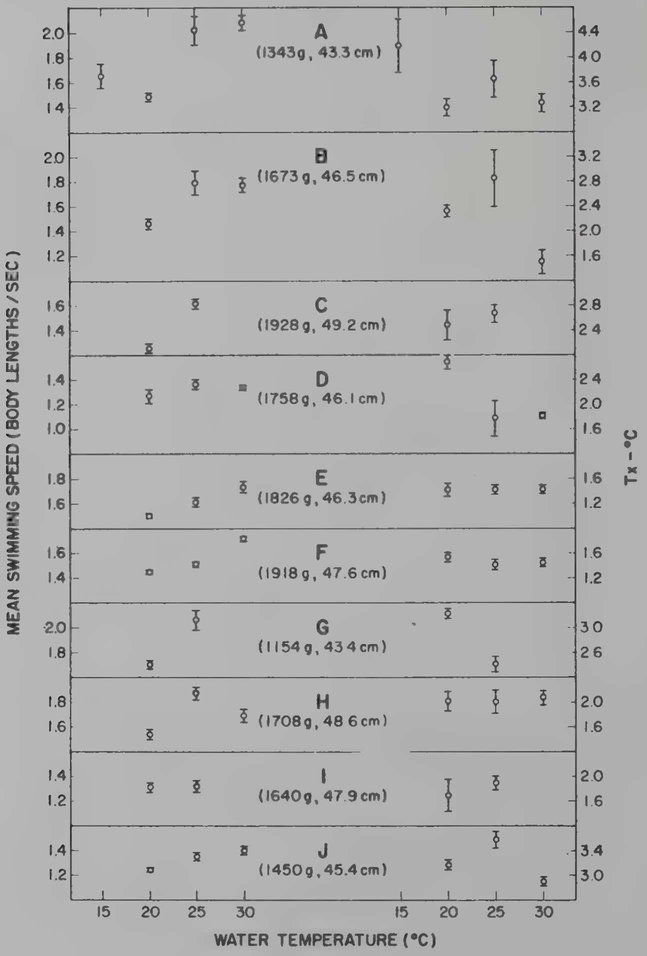

FIG. 11. Swim speed (±95% C.L.) and red and white muscle temperatures (±95% C.L.) sampled at 15°, 20°, 25°, and 30°C test temperatures. Note: fish E and F are white muscle rather than red muscle temperatures.

TABLE VI. Forcing Coefficients to Initiate Models[a]

Fish	FL (cm)	Weight (Kg)	At 25°C test temperature: Mean T_x (°C)	At 25°C test temperature: Mean speed (lengths sec^{-1})	Fraction heat loss at gills	Respiration multiplier
A	43.3	1.343	3.653	2.020	0.68	3.0X
B	46.5	1.673	2.852	1.789	0.73	2.2X
C	49.2	1.928	2.670	1.612	0.74	2.1X
D	46.7	1.758	1.766	1.355	0.76	1.7X
E (white)	46.3	1.826	1.420	1.610	0.83	1.3X
F (white)	47.6	1.918	1.409	1.510	0.83	1.3X
G	43.4	1.154	2.407	2.057	0.82	2.0X
H	48.6	1.708	2.023	1.874	0.84	1.6X
I	47.9	1.640	1.902	1.321	0.77	2.0X
J	45.4	1.450	3.576	1.348	0.53	3.8X

[a] *Theoretical model was forced to fit mean T_x and mean swim speed at 25°C by reducing the assumed 50% heat loss at the gills to appropriate levels. Empirical model was forced by adjusting the assumed respiration relationship (muscle respiration rate = 2 × whole body respiration rate) to appropriate levels.*

which would mean that the effectiveness of the heat exchanger varies from 0.47 to 0.17. According to the empirical model, muscle respiration rate varies from 1.3 times to 3.8 times that of whole fish respiration rate. Two fish carried probes in their white muscle; the T_x was predictably lower. Consequently more heat was indicated as lost via gills and lower multipliers found.

Use of these forced predictors of T_x and the exponential smoothing function (Neill and Stevens, 1974) enabled us to predict body temperatures from time series of water temperature and activity. Thus

$$T_{rm_i} = T_{e_i} - (T_{e_i} - T_{rm_{i-1}})\, e^{-k\Delta t}$$

where

$T_e = T_a + T_x$;

Δt = time interval, sec.

A computer program was written to determine T_{rm_i} at 5 min intervals and to plot expected body temperature (T_{rm_i}), observed body temperature (telemetered), swim speed, and water temperature. Both the theoretical and the empirical models fit the observed data with surprising accuracy.

When both observed and expected temperatures were available (during periods of lap swimming) goodness-of-fit was compared by calculating mean squared residuals

$$\text{m.s.r.} = \frac{\Sigma\ (T_{rm_i} - T_{o_i})^2}{n-2}$$

where

m.s.r. = mean squared residuals, $°C^2$;

T_{o_i} = observed body temperature, i th interval, °C;

T_{rm_i} = expected body temperature, i th interval, °C;

n = number of observations.

There was little difference in the ability of both models to track observed body temperatures (Table VII). In some fish one model worked better than in others and no pattern was apparent. However, fit was noticeably better for both models in the two fish monitored for white muscle temperature. Perhaps small changes in activity affect temperature less in the white muscle. During the experimental series, we have no records of fish swimming over 2.5 lengths sec^{-1}; presumably no white muscle contribution and anaerobic metabolism were required. Goodness-of-fit was also markedly improved with larger fish. Again, the increased thermal inertia of large fish might have contributed to damp small changes in activity.

As noted earlier, both models were forced to fit the observations by setting constants so that the average swim speed and body temperature were predicted at 25°C; this assumed that no thermoregulatory changes occurred in model constants as a result of changes in environmental temperature. The theoretical model allowed a test of this assumption. If a thermoregulatory response was occurring, a simple mechanism would be to allow more heat to be lost via the gills when environmental temperatures increased. Although there are many other ways in

TABLE VII. Mean Squared Residuals to Compare Goodness of Fit of Each Model

	Mean squared residuals		
Fish	Empirical ($°C^2$)	Theoretical ($°C^2$)	Number of observations
A	0.2973	0.5505	328
B	0.8764	0.8036	490
C	0.1949	0.2231	100
D	0.1581	0.2014	584
E (white)	0.0611	0.0623	492
F (white)	0.0460	0.0478	668
G	1.0319	1.2154	228
H	0.3949	0.4660	464
I	0.3406	0.3117	174
J	0.3937	0.3374	492

which the fish may become more thermally efficient with increases in water temperature, for the moment we will assume that uncoupling of the heat exchanger represents the simplest solution. When the amount of heat lost via the gills necessary to fit mean activity and observed body temperature at each of the three treatment temperatures was calculated, the trend was for a greater predicted heat loss at higher temperatures (Table VIII). This trend was poorly defined in white muscle; this is not surprising since the theoretical model heat loss parameter is designed for heat loss from the center of the cylinder.

TABLE VIII. Fraction of Heat Loss at Gills as a Function of Water Temperature

Fish	15°C	20°C	25°C	30°C
A	0.53	0.58	0.68	0.72
B	--	0.72	0.73	0.86
C	--	0.66	0.74	--
D	--	0.66	0.76	0.75
E (white)	--	0.89	0.83	0.85
F (white)	--	0.81	0.83	0.85
G	--	0.70	0.82	--
H	--	0.80	0.84	0.87
I	--	0.73	0.77	--
J	--	0.53	0.53	0.64

E. Thermoregulation in Skipjack Tuna

Thermoregulation is supported by the work of Barrett and Hester (1964), Carey and Teal (1969), and Linthicum and Carey (1972). Furthermore, theoretical considerations alone suggest there must be some mechanism to sink heat at high activity rates and retain it at low. Some mechanism must be employed by the fish to increase thermal efficiency to get more thrust for less heat retained. If heat production is indeed proportional to a high exponent of velocity (and there is no reason to suppose that it is not considering abundant experimental work) forced convection at the lateral surface is insufficient to dissipate the heat produced at even aerobic activity levels. Using relationships formulated by Sharp and Vlymen (this volume) and Sharp and Francis (1976), excess temperatures can be calculated for a 70 cm FL skipjack tuna and plotted with swim speed as the dependent variable (Fig. 12). Using coefficients of total drag that approach 0.01, excessive temperatures are developed at speeds as low as 3 lengths sec^{-1}. A 10° excess is reached--which would limit fish to below 25°C water (Neill *et al.*, 1976)--even with a heat exchanger efficiency of only 25%. If the lowest conceivable coefficients of total drag are used (.001) damaging temperatures are reached at 6 lengths sec^{-1}

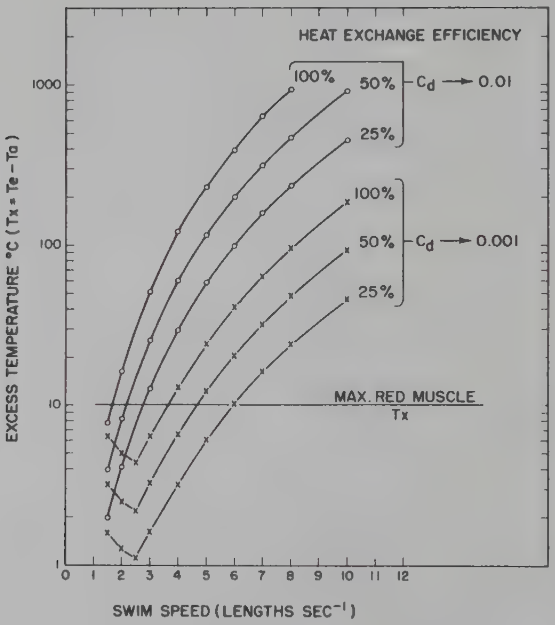

FIG. 12. Excess temperatures (T_x) calculated for a 70 cm skipjack tuna by methods of Sharp and Vlymen (this volume) at three levels of heat exchanger efficiencies and at two coefficient of drag minimums. T_x maximum of about 10°C is assumed for a fish swimming in 25°C water.

activity levels. We tracked a fish of this size swimming at this rate for more than 30 min.

Clearly then, skipjack tuna have a twofold problem; they must conserve heat during periods of low activity (or during their early life history) and they must dissipate excess heat during periods of moderate to high activity (or when they are larger) to avoid muscle temperatures in excess of 35°C (Neill *et al.*, 1976). We would like to suggest a mechanism.

As activity increases in a skipjack tuna, body temperature rises but it does not rise as fast as would be predicted by a model of forced convection at the lateral surface. Two mechanisms intervene: (a) swimming efficiency increases and (b) the heat exchanger allows proportionally more heat to escape to be dissipated at the gills. The latter would seem to be of a physiological process rather than a strictly mechanical one since at higher environmental temperatures more heat is also lost at the gills. These two mechanisms work to limit temperature during sustained, aerobic swimming. As swimming speed increases to levels where the white muscle must be called upon, anaerobic processes of energy production occur. Thermal efficiency may be much higher under these conditions; possibly lactate is excreted or at least retained until later recovery periods. During white muscle activity (perhaps now red muscle heat production has reached saturation) heat production may be less of a problem: (a) thermal efficiency may be greater; and (b) heat production occurs throughout a much greater (80%) muscle mass which is located closer to the lateral surface where forced convection removes heat more efficiently. The parabolic temperature profile used as a model for the Sharp and Vlymen forced convection simulation is replaced by the situation in which temperature is relatively homogeneous throughout the muscle mass. Upon capture, the animal is removed from the water and no heat is lost via the gills. But activity and thus heat production remain the same if not higher. The parabolic temperature profile reasserts itself due to the decreased central heat loss.

So for the moment, we suggest it would be safer to assume that skipjack tuna (and possibly other tunas with central exchangers) do physiologically thermoregulate; they have some mechanism to conserve heat during some periods of their life and to shunt heat to be dissipated at the gills during other periods and conditions. A central heat exchanger whose efficiency could be changed represents a simply implemented mechanism; so simple that it is hard to believe such an important evolutionary step has not been taken.

7810

The Lake Washington Ecosystem: The Perspective from the Fish Community Production and Forage Base[1]

D. M. EGGERS

Fisheries Research Institute, College of Fisheries, University of Washington,
Seattle, Wash. 98195, USA

N. W. BARTOO,[2] N. A. RICKARD, R. E. NELSON[3]

Washington Cooperative Fishery Research Unit, College of Fisheries,
University of Washington, Seattle, Wash. 98195, USA

R. C. WISSMAR, R. L. BURGNER, AND A. H. DEVOL

Fisheries Research Institute, College of Fisheries, University of Washington,
Seattle, Wash. 98195, USA

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In Lake Washington, fish production through detritus-based food chains is substantially greater than fish production through the grazing food chain. The lack of significant grazing by fish on the zooplankton is a consequence of both piscivore predation and conditions in the planktivore spawning environment. At low planktivore abundance, squawfish may switch to benthos feeding, exploiting the abundant prickly sculpin. At high planktivore abundance, squawfish feed more heavily on planktivores. Thus, even when reproductive success of planktivores is good, swamping of the squawfish population does not occur and depensatory mortality due to squawfish predation prevents planktivore abundance from increasing to the point where zooplankton resource depletion would occur. Benthic–littoral species are vulnerable to predation essentially only as larva and juveniles. They avoid predation by occupying littoral and epibenthic refugia. Recruitment to the adult population from these refugia may be sufficient to account for the greater rate of benthos exploitation by fish relative to the rate of zooplankton exploitation by fish. *Neomysis* is an important component of the Lake Washington fish production, since potentially *Neomysis* is a regulating agent on the zooplankton, and reduction in *Neomysis* predation on zooplankton, due to decreasing abundance and a deeper vertical distribution, may be partly responsible for the recent reappearance of *Daphnia*. The response of the fish community to trophic changes in Lake Washington has been slight. No consistent trends in the growth of fish utilizing zooplankton were observed. However, annual growth increments of consumers utilizing the benthic detrital food chain have declined with sewage diversion. The insights gained from analyzing the Lake Washington fish community structure and the Lake Washington carbon budget corroborate the above response of the fish community to trophic changes. Planktivores are predator-controlled and not able to deplete zooplankton resources, and thus would be insensitive to alterations in standing crop of zooplankton. On the other hand, benthic–littoral fish are more resource-limited and would be expected to respond to alterations in their forage base.

Key words: ecosystem, fish, production, Lake Washington, eutrophication, predation

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[1] Contribution No. 336 from the Coniferous Forest Biome, and Contribution No. 493 from College of Fisheries, University of Washington, Seattle, Wash.

[2] Present address: National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, Calif. 92038, USA.

[3] Present address: National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Resource Ecology and Fisheries Management, 2725 Montlake Blvd. East, Seattle, Wash. 98112, USA.

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Dans le lac Washington, la production de poissons par l'intermédiaire des chaînes alimentaires à base de détritus est beaucoup plus forte que celle que donne la chaîne alimentaire à base de broutage. Le fait que les poissons ne broutent pas à un degré significatif le zooplancton est le résultat tant d'une prédation sur les piscivores que des conditions de l'environnement reproducteur des planctivores. Quand les planctivores sont peu abondants, la sauvagesse peut changer et adopter un mode d'alimentation benthique, se nourrissant de chabots visqueux abondants. Quand les planctivores sont abondants, la sauvagesse mange davantage de planctivores. C'est pourquoi, même quand les planctivores ont une reproduction réussie, il n'y a jamais submersion de la population de sauvagesses et la mortalité anticompensatoire causée par la prédation des sauvagesses empêche les planctivores d'augmenter au point où la ressource zooplanctonique s'épuise. Ce n'est qu'aux stades de larves et de jeunes que les espèces bentho–littorales sont vulnérables à la prédation. Elles évitent les prédateurs en occupant des refuges littoraux et benthiques. Les recrues qui quittent ces refuges pour se joindre à la population adulte peuvent suffire à expliquer le taux plus élevé d'exploitation du benthos par les poissons comparativement à leur taux d'exploitation du zooplancton. *Neomysis* est un composant important de la production de poissons du lac Washington, car l'espèce est un agent possible de régulation du zooplancton et il se peut qu'une diminution de prédation de *Neomysis* sur le zooplancton, par suite d'une abondance moindre et d'une distribution verticale plus en profondeur, soit responsable de la récente réapparition de *Daphnia*. La communauté ichtyologique n'a que très peu réagi aux changements trophiques qui se sont produits dans le lac Washington. Nous n'avons observé aucune tendance régulière dans la croissance des poissons se nourrissant de zooplancton. Cependant, les augmentations annuelles de croissance des consommateurs se nourrissant à même la chaîne alimentaire à base de détritus benthiques ont diminué avec le détournement des eaux usées. L'analyse de la structure de la communauté ichtyologique du lac Washington et du budget du carbone de ce lac est en accord avec cette réponse de la communauté ichtyologique aux changements trophiques. Les planctivores sont contrôlés par les prédateurs et ne peuvent épuiser les ressources zooplanctoniques, et seraient ainsi insensibles aux changements dans la biomasse de zooplancton. D'autre part, les poissons bentho–littoraux sont plus limités par la ressource et l'on s'attendrait qu'ils réagissent à des changements dans la biomasse des organismes fourrage.

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THIS paper presents the Lake Washington ecosystem from the perspective of total fish community production and the respective contributions of forage base groups of zooplankton, mysids, benthos, and fish to this production. The objective is to provide insight into the response of ecosystem components to changes in lake trophic state and into the determinants of fish community structure. This study provides information for comparison with other ecosystems of differing trophic states and perturbational histories. Loftus and Regier (1972) have suggested that comparative approaches are useful because they provide contrasts for drawing and testing inferences regarding fish community response to stressed and unstressed conditions. Lake Washington is particularly suited for ecosystem studies because of its unique perturbation history. Lake Washington is a lowland mesotrophic lake lying adjacent to Seattle and is well known as a case history in eutrophication and subsequent recovery after diversion of treated sewage (Edmondson 1972a, b, 1974a, 1977; Chasan 1971).

Study Area

Lake Washington is a warm monomictic lake. Stratification occurs from June through October, and the thermocline is typically located in the 10–20-m interval. Surface water temperatures range from 4 to 6°C in winter to over 20°C in summer. Physical characteristics of Lake Washington are summarized in Table 1.

Two major tributaries flow into Lake Washington. The Cedar River entering the lake at the south end contributes 55% of the inflow, and an additional 35% is furnished by the Sammamish River at the north. Several smaller streams contribute another 10% of the water income. Prior to 1916, the main inflow to Lake Washington was through the Sammamish River and outflow was through the Black River to Puget Sound. With construction of the Chittenden Locks and the Lake Washington ship canal, joining Lake Washington and Puget Sound through Union Bay and Lake Union, additional water was needed for operation of the locks. Accordingly, the Cedar River was diverted into Lake Washington and the original outlet was blocked.

Residential development has occurred along most of the 115-km shoreline. Bulkheads and docks have altered these areas, with the exception of areas designated as parks and the shorelines with wide littoral areas. The lake has shallow areas in bays and river mouths, but most shore areas are relatively steep.

There are 29 resident or transient species of fish found

TABLE 1. Physical characteristics of Lake Washington (from Anderson 1954 unless otherwise indicated).

Maximum depth (m)	65
Mean depth (m)	33
Area (km²)	87.6
Volume (km³)	2.88
Length (km)	35.1
Mean width (km)	2.4
Elevation (m)	4.3
Turnover rate of lake volume (yr^{-1})	2.9
Net sedimentation rate for 1958–74 ($mm \cdot yr^{-1}$)[a]	5.3

[a] Birch (1976).

in Lake Washington (Wydoski 1972). Wydoski lists the following 12 resident fish species as either common or abundant: prickly sculpin (*Cottus asper*), juvenile sockeye salmon (*Oncorhynchus nerka*), peamouth (*Mylocheilus caurinus*), northern squawfish (*Ptychocheilus oregonensis*), yellow perch (*Perca flavescens*), longfin smelt (*Spirinchus thaleichthys*), threespine stickleback (*Gasterosteus aculeatus*), largescale sucker (*Catostomus macrocheilus*), brown bullhead (*Ictalurus nebulosus*), black crappie (*Pomoxis nigromaculatus*), largemouth bass (*Micropterus salmoides*), and carp (*Cyprinus carpio*).

The first seven species in this list are the most common and their abundance, annual production, and diet are dealt with here. The last four species are relatively restricted, being found in weedy bays and undeveloped shoreline that constitute only a small portion of the total fish habitat of Lake Washington because of urbanization and shoreline development (Hockett 1975). Suckers are a long-lived, slow-growing species that consume only benthos (Scott and Crossman 1973) and are common throughout the lake. Largescale suckers are less abundant than squawfish and are a minor component of the total fish production of the lake (Bartoo 1972).

Materials and Methods

All fishing methods were selective with respect to both size of fish and habitat sampled. To obtain comparable population statistics for all age-classes of several species of fish, it was necessary to use several pieces of gear, and to obtain the catchability coefficient, selectivity, and the size or age at which fish were fully recruited for each type of sampling apparatus.

A long-term sampling program was not undertaken specifically to monitor the response of several populations to trophic changes in Lake Washington. Instead, we utilized the results of several diverse studies, most of which were individual efforts, for estimates of the abundance of each age-class of the major fish species in Lake Washington. Then we assessed the fish populations quantitatively in terms of annual production, growth, and prey consumption rates.

This study summarizes and synthesizes the work of many people over the years 1962–76. Three sampling methods were used.

LIMNETIC SAMPLING

Limnetic sampling with midwater trawls and hydroacoustic gear was targeted at juvenile sockeye salmon, longfin smelt, and threespine stickleback. The limnetic fish populations in Lake Washington have been sampled since 1962 (Dryfoos 1965; Woodey 1971; Dawson 1972; Traynor 1973; Doble 1974; Moulton 1974). Acoustic estimation techniques have evolved over this period (Thorne 1970, 1971, 1972, 1973; Thorne and Lahore 1969; Thorne and Woodey 1970; Thorne et al. 1972, 1974). Also, population estimates can be derived solely from the trawl catch per unit effort (Traynor 1973).

Catches from midwater trawl hauls were used to determine length (fork length for sockeye, and standard length for stickleback and smelt), weight, and species composition (used in conjunction with acoustic surveys). During the years 1967–71, trawl surveys were incomplete. The catches from those strata not sampled were considered as missing data and were estimated by simple linear regression from those strata sampled. The population estimates presented here are simple averages of all point estimates (from acoustic as well as net sampling) made December through January when the limnetic fish were fully recruited to the gear.

Neomysis awatchensis were caught in substantial numbers during the nocturnal sampling with the Isaacs–Kidd midwater trawl (IKMWT). A 2-m IKMWT was used during the early period May 7, 1962 to October 21, 1964, and a 3-m IKMWT thereafter. To standardize these catch data, an effective cross-sectional area for the two nets was estimated using information from Banse and Semon (1963) and Friedl (1971). The population estimation technique for *Neomysis* was patterned after the net estimation technique for limnetic fish (Traynor 1973). Missing data due to incomplete trawl surveys were similarly estimated.

The diet composition of limnetic fish species in Lake Washington was determined from diel sampling at roughly 2-mo intervals, November 1974–October 1975. Sampling methods and means of determining numerical diet composition are given in Doble and Eggers (1978). The mean body carbon content for each prey species found in the diet was determined by measuring the mean length of each prey species and then converting that length to total body carbon from relationships given by M. L. Perkins (Water and Air Resources, Dept. Civil Engineering, Univ. Washington, Seattle, Wash., personal communication). Using this information, we converted the numeric diet composition to diet composition by prey body carbon content. This analysis was performed on individual fish stomachs. Stomach contents were pooled by fish age-class and sampling date and then averaged to give mean diet composition by prey body carbon content.

GILLNET SAMPLING

Gillnet sampling was targeted at peamouth, squawfish, and yellow perch. The primary gear used for sampling these species was monofilament gill nets. Panels of mesh from 2.54 to 12.70 cm, in 1.27-cm increments, were connected in random order to form the nets. Gill nets were fished in either a horizontal or a vertical mode. Details of the horizontal gillnet construction are given by Nishimoto (1973) and Hansen (1972). Horizontal gill nets sample the stratum within 1.83 m of the bottom. Vertical gill nets sampled the entire water column. Details of the vertical gillnet construction are given in Hansen (1972), Bartoo 1972), and Bartoo et al. (1973). Data collected consisted of standard life history information — length, weight, sex, gonad weight, otolith or scale sample, and stomach sample.

Population estimates based on the horizontal and vertical gillnet sampling were given by Bartoo (1977). The estimated abundance of age 1+ peamouth from limnetic sampling was extrapolated to population estimates of peamouth, northern squawfish, and yellow perch from information on relative abundance; horizontal, vertical, and regional distribution; age composition; and age structure from gillnet catches. The gillnet catch data were adjusted for selectivity by a procedure modified from Hamly (1975) using data given by Hansen (1972). Abundances of age 0+ peamouth, age 0+ and 1+ squawfish, and 0+ yellow perch, not yet recruited to the gillnet sampling gear, were extrapolated from the abundance of older age-classes based on rate of natural mortality.

BAITED MINNOW TRAP SAMPLING

Sampling with baited minnow traps was targeted at prickly sculpin. Largescale sucker fillets were used as bait. Data from this sampling consisted of standard life history information — length, weight, sex, gonad weight, otolith sample, and stomach sample.

Population estimates based on the baited minnow trap sampling are also given by Rickard (1978). Rickard determined the mean trapping area of each trap by an experiment in which strings with traps at various distances apart were fished. The CPUE increased asymptotically as the distance between traps increased allowing estimation of mean trapping area. The catches were adjusted for selectivity using a model described by Rickard (1978) and then extrapolated to a population estimate using the mean trapping area and area of the particular stratus fished.

GROWTH, PRODUCTION, AND BIOMASS

Seasonal growth curves by weight for sockeye, smelt, and stickleback were estimated from limnetic sampling. Sample sizes were insufficient for directly constructing seasonal growth curves for all age-classes of squawfish, peamouth, yellow perch, and prickly sculpin. However, the mean annual growth increments (in length) for all constituent age-classes were determined for peamouth (Nishimoto 1973), squawfish (Olney 1975), yellow perch (Nelson 1977), and sculpin (Rickard 1978) by the back-calculation method of determining mean length at annulus formation from growth zones on scales or otoliths (Tesch 1971; Chugunova 1963). For some year-classes, sample sizes were sufficient for direct estimation of seasonal growth curves by length or weight. The monthly growth increments in length or weight were converted to percentage of the annual growth increment. Bartoo (1977), Rickard (1978), and Nelson (1977) found no difference in the seasonal growth pattern expressed as percentage of annual growth increment for the following groups:

1. All age-classes of peamouth (weight).
2. Age 2–4 squawfish (immature) (length).
3. Age 5 and older squawfish (mature) (length).
4. Age 2 and older yellow perch females (mature) (length).
5. Age 2 and older yellow perch males (mature) (length).
6. Age 1+ yellow perch (immature) (length).
7. All age-classes of prickly sculpin (weight).

The data for each of these groups were pooled to give a curve of monthly growth increments. From this information and the mean annual growth increments a seasonal growth curve for the above age-classes and species was computed. Seasonal growth curves were not available for age 0+ and 1+ squawfish and age 0+ yellow perch. For those groups growth was assumed to be linear. If the measured monthly growth increments were in units of length, the derived seasonal growth curve (in units of length) was converted to units of weight via length–weight relationships given in Olney (1975) and Nelson (1977). If the measured monthly growth increments were in units of weight, the annual growth increments from scale studies were converted to weight based on the technique of Pienaar and Ricker (1968) and weight–length relationships given by Nishimoto (1973) and Rickard (1978).

Production is defined here as the total amount of tissue elaborated in the population or community under study in a given period of time (Allen 1971). That is,

$$P = \int_{T_1}^{T_2} N_t \frac{dW_t}{dt}\, dt \tag{1}$$

where P is the production, T_1 is the beginning of the time period, T_2 is the end of the time period, N_t is the number of fish in the population at time t, and dW_t/dt is the instantaneous rate of growth in weight. To compute production, a model is needed for abundance (N_t) and a model for growth (W_t). From analyses of catch curves, Bartoo (1977) found mortality to be an exponential decay function for peamouth, squawfish, and yellow perch. Similar results were found for sculpin (Rickard 1978) and juvenile sockeye (Bryant 1976). Thus,

$$N_t = N_o \exp(-mt) \tag{2}$$

where m is the instantaneous rate (month^{-1}) of natural mortality. To simplify the computation of annual production, the year was divided into monthly intervals where growth was linear; hence dW_t/dt is constant during those intervals. Substituting equation (2) into equation (1) and integrating yields

$$P = \sum_{i=1}^{12} \Delta W_i N_i \left[\frac{1 - e^{-m}}{m}\right] \tag{3}$$

where ΔW_i is the monthly growth increment and N_i is the population abundance at the beginning of month i. P was computed for each species and constituent age-class. Mean annual biomass (B) was similarly computed for each species and constituent age-classes:

$$B = \frac{\sum_{i=1}^{12} W_i \mathrm{N}_i \left[\frac{1 - e^{-m}}{m}\right]}{12} \tag{4}$$

where W_i is the mean weight during month i.

Results

PARTICULATE ORGANIC CARBON BUDGET

To relate the Lake Washington fish community to the trophic economy by the lake, we estimated the dietary components of the annual fish production. To make this estimate we had to construct the annual pattern of abundance, growth, and diet for each major fish species and respective age-class.

Mean annual biomass and production of the limnetic species were computed for the period January 1, 1972

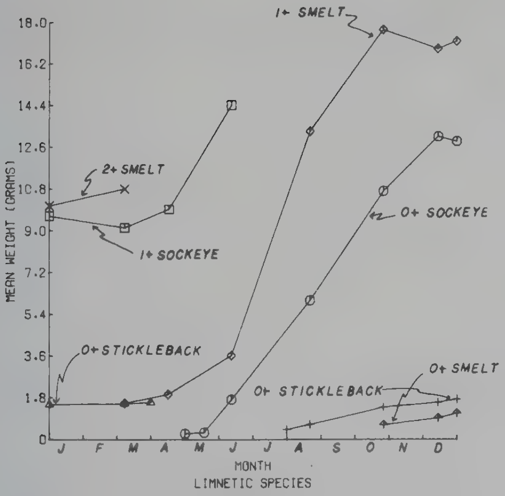

FIG. 1. Seasonal growth trajectories for relevant year-classes of the limnetic fish species in Lake Washington during 1972.

to December 31, 1972. In Lake Washington, threespine stickleback and longfin smelt mature at age 1 and age 2, respectively, and die after spawning. This period encompassed the growth (Fig. 1) of 1970 and 1971 year-classes of juvenile sockeye salmon (migrated spring 1972 and 1973, respectively); 1971 and 1972 year-classes of threespine stickleback (matured spring 1972 and 1973, respectively); and 1970, 1971, and 1972 year-classes of longfin smelt (matured late winter 1972, 1973, and 1974, respectively). Using the respective instantaneous rates of natural mortality (Table 2), the abundances of the limnetic fish species during this period were extrapolated from the winter abundance before maturity or outmigration of the 1970, 1971 year-class of juvenile sockeye salmon; 1971, 1972 year-class of stickleback; and 1970, 1971, 1972 year-classes of longfin smelt.

Data on abundance, growth, and diet of the benthic–littoral fish species were collected from 1971 to 1975. Population abundances were essentially point estimates (Fig. 2). Because these species are long-lived, and, except for squawfish, show no extensive variation in year-class strength (Fig. 2), the bias due to annual variation in abundance is negligible. The abundance of the youngest age-classes of peamouth, squawfish, and yellow perch not yet recruited to the gill nets was estimated by extrapolating from the abundance of the older age-classes, taking into account the instantaneous rates of natural mortality (Table 2). Growth was estimated by extrapolating size at annulus formation (Table 3) by monthly values of mean annual growth increments. Most of the production and biomass of fish in Lake Washington is prickly sculpin (Table 4).

TABLE 2. Instantaneous (day^{-1}) rate of natural mortality for Lake Washington fish populations.

Population	Mortality	Source
Juvenile sockeye		
1970 year-class	−0.00290	Bryant (1976)
1971 year-class	−0.00274	Bryant (1976)
Smelt	−0.00282	Avg of the sockeye mortality rates
Stickleback	−0.00282	Avg of the sockeye mortality rates
Peamouth	−0.00397	Bartoo (1977)
Squawfish	−0.00074	Bartoo (1977)
Yellow perch	−0.00156	Bartoo (1977)
Prickly sculpin	−0.00295	Rickard (1978)

TABLE 3. Mean weight (grams) at annulus formation for various species of fish in Lake Washington.

Age	Peamouth	Squawfish	Prickly sculpin	Yellow perch males	Yellow perch females
1	9	—	1.0	8.8	10
2	38	26	7.2	52	65
3	81	94	16	125	171
4	132	187	26	188	281
5	190	293	41	242	376
6	240	408	60	282	454
7	303	528	81	328	502
8	352	650	110		
9	408	773			
10		897			
11		1,021			
12		1,145			
13		1,269			
14		1,393			
15		1,517			
16		1,641			
17		1,765			
18		1,889			
19		2,013			
20		2,137			
21		2,261			
22		2,385			

A great number of prey items are available to Lake Washington fishes. To provide a simple picture of carbon flow through water column and benthic communities, as well as to avoid a confusing presentation involving tens of prey species, the prey items in the diet were grouped according to zooplankton, benthos, mysids, and fish (Fig. 3 and 4). The diet of age 2+ peamouth is strictly benthos (Nishimoto 1973; Shanbhogue 1976).

The relative contribution of the zooplankton, mysids, benthos, and fish prey items to fish production was estimated by grouping fish according to similar feeding habitat and diet composition (Table 5). These functional groups ranged from strictly limnetic fish feeding on zooplankton and emergent insects to strictly benthic

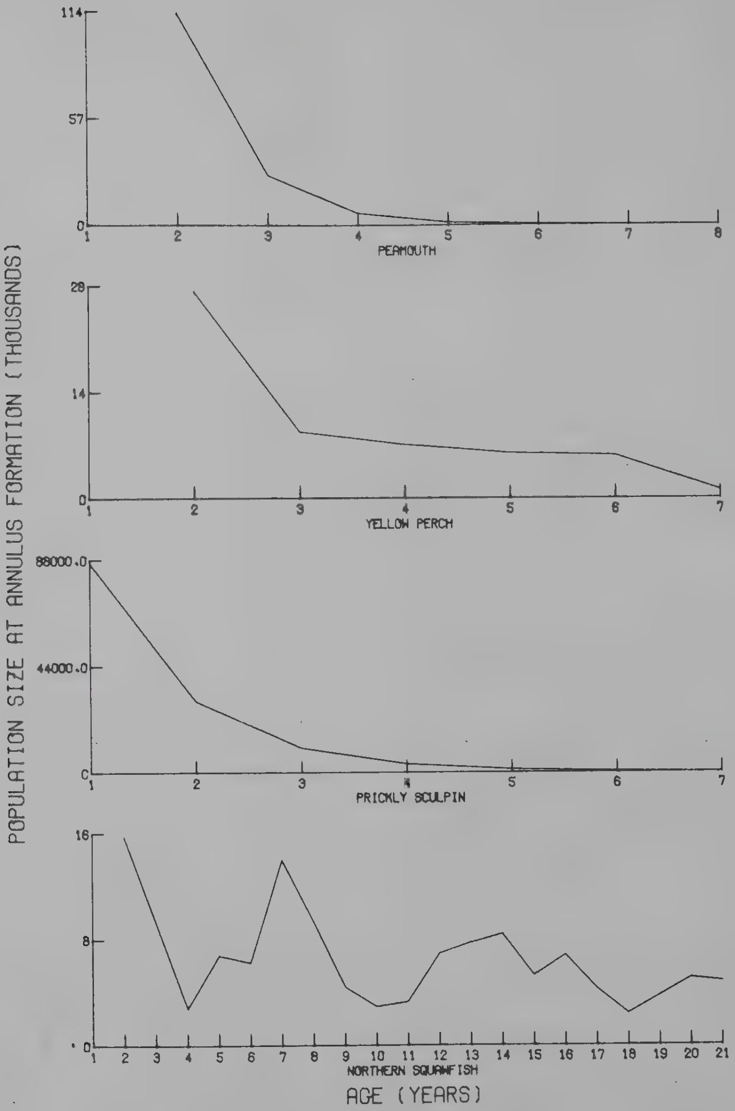

FIG. 2. Abundance at annulus formation for constituent age-classes of peamouth, yellow perch, prickly sculpin, and northern squawfish in Lake Washington.

feeding fish as evidenced by a diet of benthos, mysids, and bottom fish (sculpin). Older age-classes of sculpin were cannibalistic and can be considered piscivores as well as benthic feeders. The facultative piscivores (older age-classes of yellow perch and squawfish) feed in the water column as well as on the bottom.

The relative contribution of each prey group to fish production was estimated by partitioning the production

TABLE 4. Annual production and mean annual biomass of Lake Washington fishes.

Species	Annual production (kg wet wt/yr)	Percent of total production	Mean annual biomass (kg wet wt)	Percent of total biomass	Turnover rate $\frac{P}{B}$
Prickly sculpin	6.56×10^5	83.8	5.95×10^5	72.7	1.41
Juvenile sockeye salmon	4.88×10^4	6.2	4.07×10^4	5.0	1.19
Peamouth	2.65×10^4	3.4	1.98×10^4	2.4	1.34
Longfin smelt	2.68×10^4	3.4	3.07×10^4	3.8	0.87
Northern squawfish	1.55×10^4	2.0	1.16×10^5	14.2	0.13
Yellow perch	5.51×10^3	0.7	1.14×10^4	1.4	0.48
Threespine stickleback	3.42×10^3	0.4	4.53×10^3	0.6	0.75

of each constituent age–species class in the functional group by its respective diet composition and summing (Table 6). Of the prey groups, benthos contributed most (74.3%) and fish contributed least (6.4%) to fish production.

A particulate organic carbon budget incorporating the dietary components of fish production and ration was constructed for Lake Washington (Table 7). The Lake Washington carbon budget is incomplete because of the lack of data on littoral primary production and on allochthonous inputs to the lake. Data are also inadequate for estimating production, respiration, and diet of the *Neomysis* population. Values presented in parentheses reflect only the population cropped by fish and therefore serve as a minimum estimate.

TABLE 5. Definition of the functional groups of fish used to compute the relative contribution of zooplankton, benthos, mysids, and fish prey items to fish production.

Functional group	Fish species and age composition	Feeding behavior	Diet
Obligate planktivores	Age 0+ sockeye Age 1+ sockeye Age 0+ stickleback	Limnetic	Zooplankton and emergent insects
Smelt	Age 0+, 1+, and 2+ longfin smelt	Limnetic epibenthic	Zooplankton mysids, emergent insects
Facultative benthic	Age 0 to 2+ peamouth Age 0 to 1 squawfish Age 0 to 1+ yellow perch	Benthic epibenthic limnetic	Benthos, mysids, zooplankton
Obligate benthic	Age 2+ to 8+ peamouth Age 0 to 7+ sculpins	Benthic epibenthic	Benthos, mysids, sculpins
Facultative piscivores	Age 1+ to 6+ yellow perch Age 1+ to 21+ squawfish	Limnetic benthic	Benthos, mysids, fish

The carbon budget shows that the benthic food chain is as important as water column processes to the trophic dynamics of Lake Washington, which is surprising for a deep lake where the littoral area is <20% of the lake surface area. However, fluvial and direct sedimentation inputs of carbon to the sediments appear insufficient to fuel the benthic production (Table 7). This deficiency was most likely due to unaccounted-for inputs of littoral production by periphyton and attached macrophytes.

In Lake Washington, cold littoral water sinking down the steep sides of the lake basin causes winter thermal convection currents (Syck 1964). These convection currents have been described as sufficient in magnitude to have eroded the original U-shaped Lake Washington basin to its present W shape (Gould and Budinger 1958). Thus, detrital material produced in littoral regions could be transported to profound regions of the lake.

Steele (1974) and Mills (1975) encountered imbalances in their analysis of the trophic economy of the North Sea ecosystem. They were unable to account for the observed demersal fish production from inputs to the demersal food web due to sedimentation of zooplankton fecal material if consideration was given to possible losses of bacteria respiration, metabolism of meiobenthos, and metabolism of carnivorous epifauna. At this time there are not enough studies of benthos and

TABLE 6. Dietary components of fish production (numbers in parentheses are percentage total production).

Group	Biomass (kg wet wt)	Production (kg wet wt) per year	Production due to forage items			
			Zooplankton	Benthos	Mysids	Fish
Obligate planktivores	45 200	52 200	47 640 (91.3)	4 110 (7.9)	450 (0.9)	0 (0)
Smelt	30 680	26 800	9 740 (36.3)	4 200 (15.7)	12 530 (46.8)	330 (1.2)
Facultative benthic feeders	19 610	24 460	12 000 (49.0)	11 890 (48.6)	580 (2.4)	0 (0)
Obligate benthic feeders	571 800	658 584	0 (0)	510 837 (77.6)	91 630 (13.9)	56 117 (8.5)
Facultative piscivores	127 700	19 420	0 (0)	2 790 (14.4)	2 060 (10.5)	14 570 (75.0)
Total	794 500	718 464	69 380 (8.9)	533 827 (68.3)	107 250 (13.7)	71 017 (9.1)

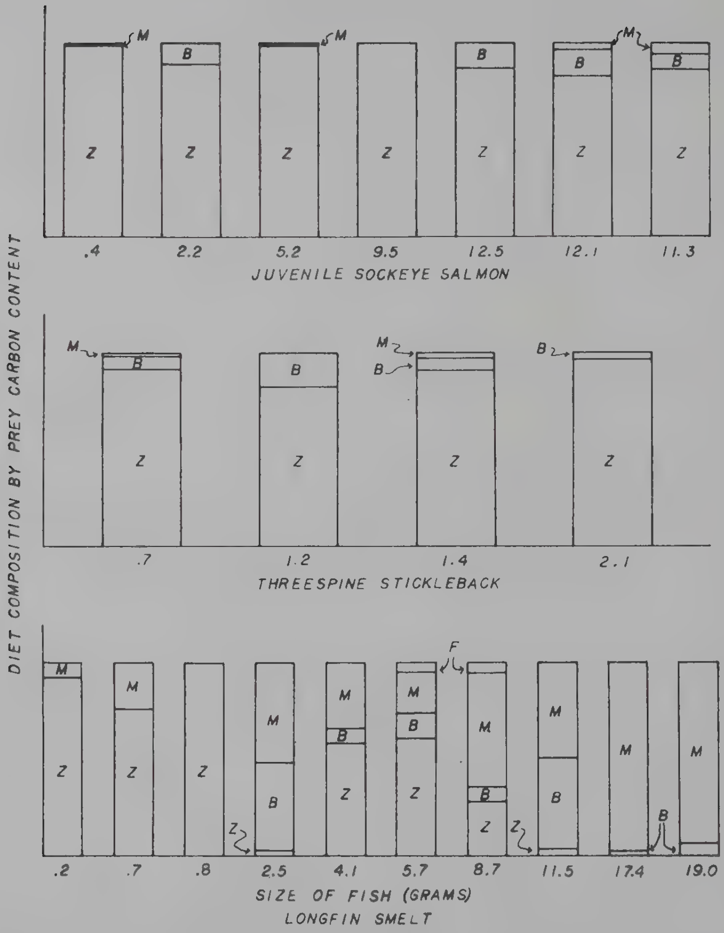

FIG. 3. Diet composition (by prey carbon content) for various sizes of juvenile sockeye, threespine stickleback, and longfin smelt in Lake Washington. These data reflect seasonal trends in diet as sampling was conducted over the period of limnetic residence for each species. The diet of sockeye (0.4–11.3 g) was collected February through February. Similarly, the diet of stickleback, (0.7–2.1 g) was collected August through February; age 0+ smelt (0.2–2.5 g) was collected August through February; and age 1+ smelt (4.1–19 g) was collected June through February. The component dietary items include zooplankton (Z), mysids (M), benthos (B), and fish (F).

zooplankton paralleling studies of fish production for generalization.

In Lake Washington the fish community is dominated by benthos feeders. The limnetic fish population was estimated to use only 1.7% of the annual zooplankton production. *Neomysis*, an organism that seemed unimportant in the catches from zooplankton sampling gear and midwater trawls, is potentially an important component of the water column food chains. In the limnetic zone of Lake Washington, *Neomysis* has declined in abundance since 1962 (Fig. 5). Abundance during 1968–71 was less than during 1974–75. The estimated mean biomass for *Neomysis* during the period November 5, 1974 to October 13, 1975 was 0.0144 g

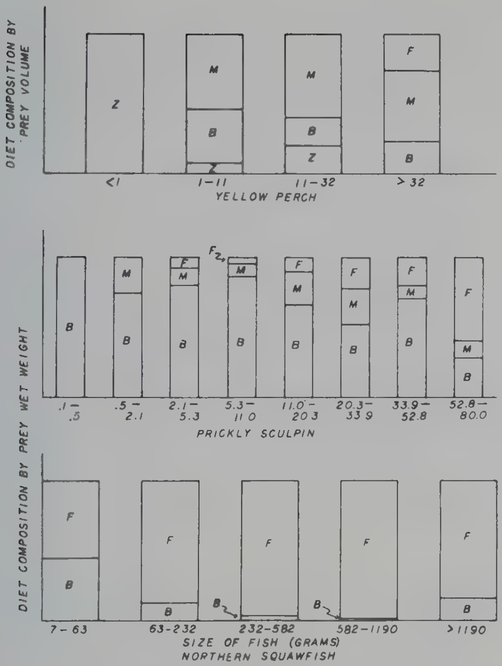

FIG. 4. Diet composition for various sizes of yellow perch (by prey volume), prickly sculpin, and northern squawfish (by prey wet weight) in Lake Washington. Data were pooled by size and do not reflect seasonal trends. The component dietary items include zooplankton (Z), mysids (M), benthos (B), and fish (F).

$C \cdot m^{-2}$. If it is assumed that the amount of *Neomysis* consumed by fish was the minimum *Neomysis* production during 1974, then the production/biomass (P/B) ratio was at least 90.3, an unreasonably high figure. The calculated P/B for Lake Washington zooplankton is 12.66. Mean zooplankton biomass during 1974 was estimated using unpublished zooplankton density (W. T. Edmondson, Dept. Zoology, Univ. Washington, Seattle, Wash., personal communication), mean length (Eggers and Doble unpublished data), and a conversion from length to body carbon content (Perkins personal communication). The high P/B for *Neomysis* indicates that we are underestimating the abundance of *Neomysis*. Accordingly, there may be sizable inshore and littoral populations not available to the sampling gear (Nelson 1977). Also, only a part of the population may be migrating from the bottom into the water column at night.

Fish consumed by yellow perch and prickly sculpin were small fish, mostly small prickly sculpin (Nelson 1977; Rickard 1978). Northern squawfish consumed both planktivorous fish (smelt, stickleback, and sockeye) as well as prickly sculpin.

RESPONSE OF THE FISH COMMUNITY TO TROPHIC CHANGES IN LAKE WASHINGTON

There were two periods of sewage input to Lake Washington. During the early part of this century, the lake received untreated sewage until diversion of the untreated effluent to Puget Sound was completed in 1936. This diversion was in response to health concerns as some communities used the lake for drinking water. Beginning in 1941, secondary sewage treatment plants dispersed effluent into Lake Washington. Because of public concern for the deterioration of the lake, diversion of the secondary treatment plant effluent began in 1963 and was completed by 1966. The phytoplankton community responded rapidly to the reduced nutrient loadings (Edmondson 1972a).

Specific components of the eutrophication history thus far documented are:

1. Nutrient loadings were 108 000 kg phosphorus in 1957; 231 000 kg in 1962; and 41 000 kg in 1974 (Edmondson 1977).
2. The summertime chlorophyll *a* concentration reached maximum levels (40 μg/L) in 1964, but were high from 1962 to 1966 (20–40 μg/L). Summertime Secchi disk readings were low (<1.5 m), 1962–67 (Edmondson 1972a).
3. Species composition of the algae has changed markedly since the period of maximum nutrient loading when filamentous blue-green algae constituted as much as 98% by volume of the phytoplankton. The percentage of blue-green algae has decreased sharply in recent years, constituting 44% of the phytoplankton in 1973 and 1974 (Edmondson 1977).
4. Zooplankton had shown no major changes in species composition until 1972 when *Daphnia* reappeared in the lake (Edmondson 1977). *Daphnia* had been observed in the 1930s (Sheffer and Robinson 1939) but not in the years 1950–72 (Edmondson personal communication). Some changes in abundance have occurred over the years but none that can be attributed to trophic changes in Lake Washington (Edmondson 1972b).

There was no consistent change in the size of juvenile sockeye at the end of the summer–fall growing season, 1966–75, that might be associated with change in the trophic condition of Lake Washington (Fig. 6). In stickleback, there was no consistent change between 1971 and 1975 in the size reached by December, even though stickleback increased greatly in abundance during the period 1967–76 while sockeye declined in abundance (Fig. 7).

Smelt exhibited cyclic abundance patterns for 1966–71 year classes, the even-numbered year-classes being more abundant than the odd-numbered year-classes. During these years, smelt exhibited density-dependent growth, the less abundant odd-numbered year-classes showing a higher growth rate (Fig. 6) than the even-numbered more abundant year-classes (Moulton 1974), a pattern that has disappeared in recent years. This pattern of growth may be related to the long-term trends in abundance of *Neomysis* (Fig. 5), which is the major prey item of smelt older than age 1. During the period of density-dependent growth (1968–71), *Neomysis* abundance was very low.

Long-term patterns of growth were estimated for peamouth (Nishimoto 1973) and for squawfish (Olney 1975) by back-calculation techniques. Nishimoto showed that back-calculated annual growth increments increased from 1962 to 1967–68 when they peaked (Fig. 8). In subsequent years, a progressive decline in growth occurred. The maximum growth rates for peamouth were observed approximately 2 yr after maximum primary production resulting from cultural eutrophication (Edmondson 1972a). Olney (1975) compared the back-calculated total length at each annulus as well as annual growth increments during the first 5 yr of growth for 1955–71 year-classes of squawfish (Fig. 9). Annual growth increments during the first 3 yr of growth increased from 1955 to 1966–68 and declined thereafter. This pattern did not hold for the 4th and 5th yr of growth. Age 0–2+ squawfish feed primarily on benthos. The historical trends in growth of squawfish correlate with those of peamouth which also feed primarily on benthos.

Although there were trends of decreasing growth in fish utilizing benthos as food following sewage diversion, comparisons of size at annulus formation for squawfish (Olney 1975), peamouth (Nishimoto 1973), and yellow perch (Nelson 1977) show that the growth achieved by these Lake Washington fishes is greater than or equal to that in other lakes.

Although growth of Lake Washington planktivores has not changed during the period following sewage diversion, abundance has. Stickleback have increased greatly in abundance during 1967–76 while sockeye have declined (Fig. 2). The decline in sockeye abundance has been attributed to high incidence of midwinter floods during the last 7 yr in the Cedar River, washing the eggs out of the gravel (Bryant 1976; Miller 1976). The increase in stickleback abundance may be due to changes in littoral environment accom-

TABLE 7. Particulate organic carbon budget for Lake Washington. (All values are given in $g \cdot m^{-2} \cdot yr^{-1}$. See footnote for explanation of source data.[a])

Water column			Benthic–littoral		
Inputs	Value	Source	Inputs	Value	Source
Allochthonous			Water column		
Fluvial	20.0	1	Sedimentation	53.0	3
Precipitation	ND		Autochthonous		
Litter	ND		Periphyton	ND	
Autochthonous			Macrophytes	ND	
Phytoplankton production	157.0	2	Total inputs	53.0	
Total inputs	177.0				
Losses			Losses		
Outflow	0.5	1	Benthic respiration	52.0	8
Sedimentation	53.0	3	Fish respiration	2.0	6
Microplankton respiration	59.0	4	Burial	35.0	9
Zooplankton respiration	48.0	5	Emergence	ND	
Neomysis respiration	ND (2.4)	7	Macrophyte and periphyton respiration	ND	
Planktivorous fish respiration	0.5	6	Total losses	104.9	
Piscivorous fish respiration	0.03	6			
Total losses	163.0				
Internal transformations			Internal transformations		
Ingestion			Ingestion		
Material ingested by zooplankton	97.0	5	Material ingested by macroinvertebrates	113	10
Material ingested by *Neomysis*	ND (4.0)	7	Macroinvertebrates ingested by fish	3.1	6
Zooplankton ingested by fish	0.33	6	Fish ingested by fish	0.5	6
Neomysis ingested by fish	0.6	6	Production		
Fish ingested by fish	0.04	6	Microbial	ND	
Production			Macroinvertebrates	16.9	10
Microbial	ND		Fish production supported by macroinvertebrates	0.8	6
Zooplankton	19.0	5	Fish production supported by fish	0.1	6
Neomysis	ND (0.6)	7			
Fish production supported by zooplankton	0.10	6			
Fish production supported by *Neomysis*	0.15	6			
Fish production supported by fish	0.01	6			

panying trophic changes in Lake Washington. Stickleback are territorial and compete for suitable spawning substrate (Scott and Crossman 1973). During periods of peak nutrient loading, littoral areas of Lake Washington had mats of blue-green algae growing on the substrate (Chasan 1971). Possibly suitable spawning substrate or rearing habitat limited the Lake Washington stickleback population before 1970.

Zooplankton showed no consistent change in abundance or species composition from 1962 (Edmondson 1972b) until 1972 when *Daphnia* sp. appeared (Edmondson 1977). Large zooplankters present in Lake Washington include *Epischura nevadensis* and *Diaphanosoma* sp. before 1972, and *Epischura*, *Diaphanosoma*, and *Daphnia* after 1972.

Planktivorous fish in Lake Washington show extreme size-selective predation, but are not sufficiently abundant to regulate the large zooplankters. The reappearance of *Daphnia* in Lake Washington may have been a response to phytoplankton succession accompanying sewage diversion. However, in addition to planktivorous fish, there is another potential zooplankton predator, *Neomysis*, that is an important contributor to fish production in Lake Washington. Its biomass ingested by fish is twice that of zooplankton ingested.

The information we have on *Neomysis* is based on nighttime midwater trawls, and indicates that since 1962 *Neomysis* abundance has decreased and that the nocturnal vertical distribution has shifted to lower strata (Fig. 6). From 1962 to 1964, when lake water transparency was much lower than at present, substantial numbers of *Neomysis* were found in the water column during the day. Although we have no information on the present daytime vertical distribution, *Neomysis* must be near the bottom because they constitute a significant portion of the diet of prickly sculpin. This is because cottids are ambush predators, with no swim bladder, and therefore can feed effectively only near the bottom. The apparent downward shift in the vertical distribution of *Neomysis* may be a response to the changing ambient light conditions in Lake Washington as a consequence of sewage diversion.

The vertical distribution of *Neomysis* in Lake Washington is consistent with the behavior of a similar species, *Mysis relicta*. The vertical distribution of *M. relicta* in Lake Huron and Lake Michigan was strongly influenced by ambient light intensity (Beeton 1960). Beeton also found that *Mysis* were deeper in the water column on moonlit nights than on dark nights. Additionally, the introduction of *Mysis* into Lake Tahoe caused a virtual disappearance of *Daphnia* from that lake (Richards et al. 1975). Lasenby and Langford (1972) found that *Mysis* in Stony Lake was a benthic detritivore by day and a voracious carnivore preying on *Daphnia* by night.

These two pieces of evidence, the vertical distribution and the apparent decline in abundance of *Neomysis*, along with the information on *M. relicta*, suggest a second cause of the reappearance of *Daphnia* in Lake

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[a] 1. Representative particulate organic carbon measurements in the Cedar and Sammamish rivers extrapolated from U.S.G.S. flow data (J. E. Richey, Fisheries Research Institute, Univ. Washington, Seattle, Wash., personal communication).

2. Phytoplankton production from ^{14}C uptake during 1974 (Devol and Packard 1978).

3. Losses of algal, fecal, and allochthonous material from the water column measured by sediment trap, March 1974 to March 1975 (Birch 1976).

4. Sum of euphotic and aphotic microplankton respiration during 1974 (Devol and Packard 1978). Respiration was measured by the activity of the respiratory electron transport system (ETS activity) (Packard 1971).

5. Net zooplankton respiration measured by ETS activity (Devol 1977). Based on summary data presented in Parsons and Takahashi (1973) and Edmondson (1974b), amount of material ingested assumed to be 2 times the respiration, and egestion was assumed to be 30% of ingestion.

6. Fish. The organic material ingested and respiration losses were estimated by simple energy budgets ($I = R + P + E$). All of the budget components are specified by gross conversion efficiency ($K = P/I$), the assimilation coefficient (α, $E = (1 - \alpha)I$), and the production (P); α was assumed to be 0.8 (Winberg 1956). Total body carbon was assumed to be 12.5% of wet weight. In the obligate planktivore, smelt, and facultative benthic functional groups, as well as age 0–1 sculpin (Table 5), K was assumed to be 0.3 (Eggers 1975). Because larger, older fish are less efficient in converting ingested material to growth (Winberg 1956), K for the obligate benthic (except age 0–1 sculpin) and facultative piscivores (except age 1+ to 21+ squawfish) was assumed to be 0.20. Squawfish are large, slow-moving top carnivores with even lower K. Age-specific respiration and egestion for squawfish were estimated using production (Table 4) and relationship of total metabolism to body size and ambient temperature given for cyprinids by Winberg (1956). These age specific estimates of I, R, and E for piscivores were attributed to water-column supported fish and benthos-supported fish based on diet composition. The whole lake production figures were converted to a per hectare basis by dividing by the surface area of the lake.

7. Minimum estimates (shown in parentheses) of ingestion, respiration, and egestion to support the production of *Neomysis* cropped by fish assumed that $I = 5P$, $E = 0.3\ I$, $K = 0.5\ I$. This budget is the same as that used for zooplankton.

8. Benthic respiration was measured for several profundal stations during September 1972 by Pamatmat and Bhagwat (1973). Since these samples were incubated at 10°C, it is necessary to convert to in situ temperature (mean annual water column temperature 15–58 m is approximately 8°C). The mean measured value of 600 kg $C \cdot ha^{-1} \cdot yr^{-1}$ was converted to 520 kg $C \cdot ha^{-1} \cdot yr^{-1}$ assuming a Q_{10} of 2.3 (Pamatmat 1971).

9. Permanent sediment burial given by Birch (1976).

10. Bissonnette (1975) gave production for Chironomidae, March 1973–March 1974. These numbers were converted from grams dry weight to kilograms carbon and multiplied by 2, since Thut (1969) found Chironomidae to constitute approximately one half of the benthos biomass. We assumed a 15% gross conversion efficiency to estimate the required food base of 1,130 kg $C \cdot ha^{-1} \cdot yr^{-1}$.

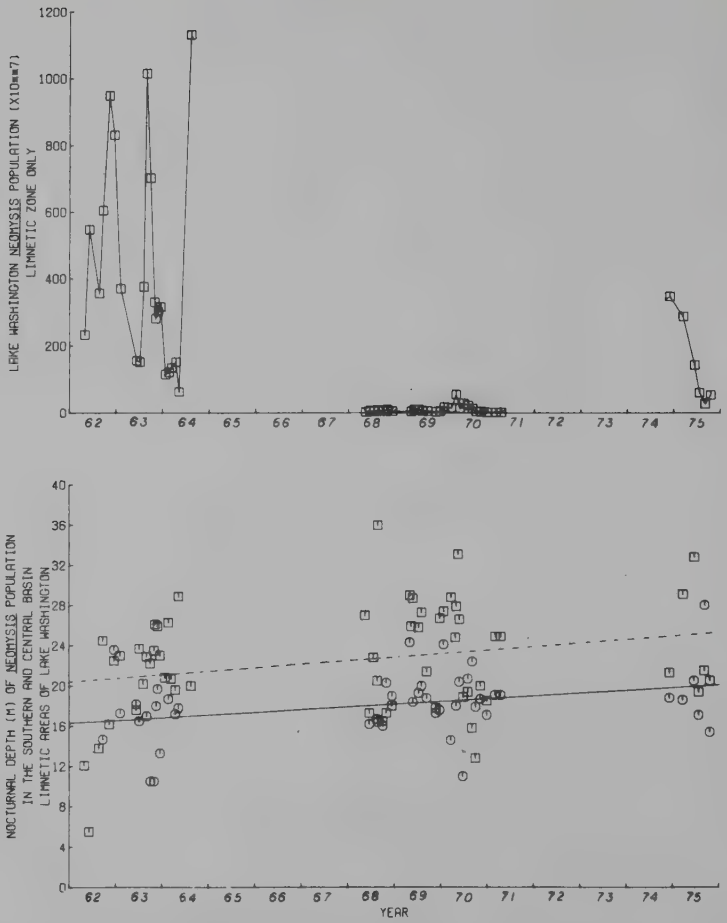

FIG. 5. Long-term trends in limnetic zone abundance (A) and the nocturnal mean depth of occurrence (B) of *Neomysis* in Lake Washington. Fitted linear regression line and data are plotted for the southern (○ solid line) and central (☐ dashed line) basins. For the southern basin, $Y = 16.3 + 0.25X$, $R = 0.316$. For the central basin, $Y = 20.4 + 0.33X$, $R = 0.252$.

Washington. After the sewage diversion and subsequent decline in primary production, the amount of algae cropped by herbivorous zooplankton apparently remained constant because there was no decrease in zooplankton abundance associated with sewage diversion. Therefore, more organic material may have been reaching the sediments during past periods of high phytoplankton production than at present. Wissmar and Wetzel (1978) in a comparison of five temperate North American lakes showed that as primary production increased, a higher fraction was available to benthic and detrital food chains. If a decrease in benthos production resulted from sewage diversion, then the decline in *Neomysis* abundance may have resulted from fish switching from benthos to *Neomysis*. This decline in abundance coupled with the downward shift of the *Neomysis* distribution may create a "refuge" in the upper water column strata for prey organisms such as *Daphnia*. *Daphnia*, like other zooplankters, are much more abundant in the upper 20 m of the lake (W. T.

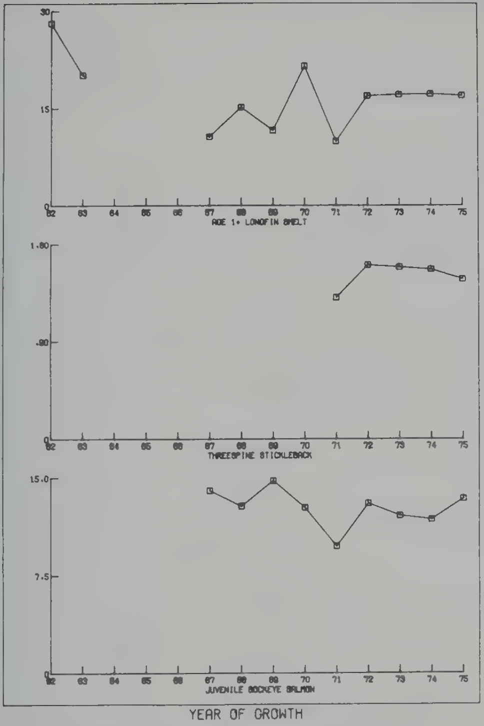

FIG. 6. Long-term trends in the mean weight in December for age 1+ longfin smelt, threespine stickleback, and juvenile sockeye salmon in Lake Washington.

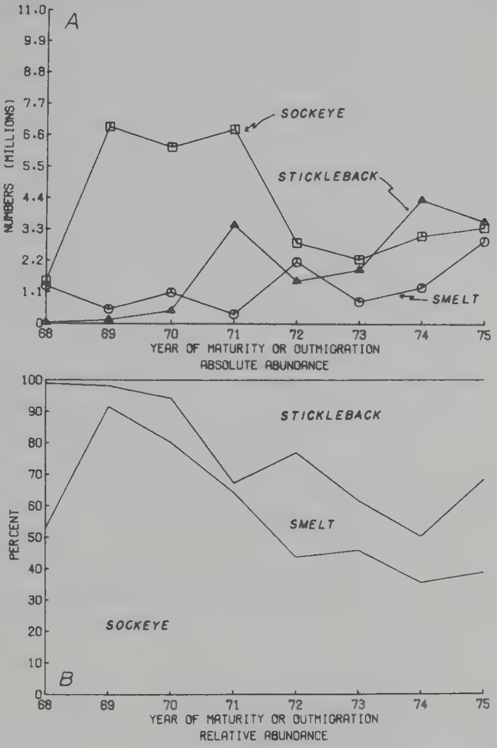

FIG. 7. Long-term trends in absolute (A) and relative (B) abundance of limnetic fish species in Lake Washington.

Edmondson personal communication). Thus, the limited evidence we have on both vertical distribution and abundance suggests that the magnitude of predation by *Neomysis* on the zooplankton community has declined since the early 1960s.

Lake Washington is unique as an experiment in eutrophication and subsequent oligotrophication with diversion of treated sewage. The response of the phytoplankton to the changing nutrient loading is well documented, but the response of Lake Washington higher consumers has not previously been documented. Detrimental effects of cultural eutrophication on salmonid communities occur at much higher nutrient loadings or more severe perturbations than occurred in the Lake Washington drainage basin (Colby et al. 1972). Detrimental effects result from depletion of hypolimnion oxygen or deforestation, erosion, damming, and pollution on the spawning tributaries.

Determinants of Limnetic and Benthic Fish Community Structure

The most significant result of this study is the determination that the fish community is dominated by benthos-consuming fish. This is surprising in a large deep lake where the area of the littoral zone is much smaller than the area of the limnetic zone. Furthermore, the magnitudes of benthos and zooplankton production are comparable (Table 7). If the prey resources were strictly limiting the fish populations, one would expect the magnitudes of benthos- and zooplankton-supported fish production to be more similar than observed in Lake Washington.

It is perhaps a truism to say that competition for resources and effects of piscivorous predation are the determinants of fish community structure. However, the structural manifestations of competition and predation are quite different and the structure of the Lake Washington fish community cannot be explained without consideration of the interaction of competition and predation.

Studies of morphological differences, habitat utilization, diet, and timing of feeding among cohabiting fish species in Lake Opinicon (Keast and Webb 1966; Keast 1970) and Lawrence Lake (Werner et al. 1977; Hall

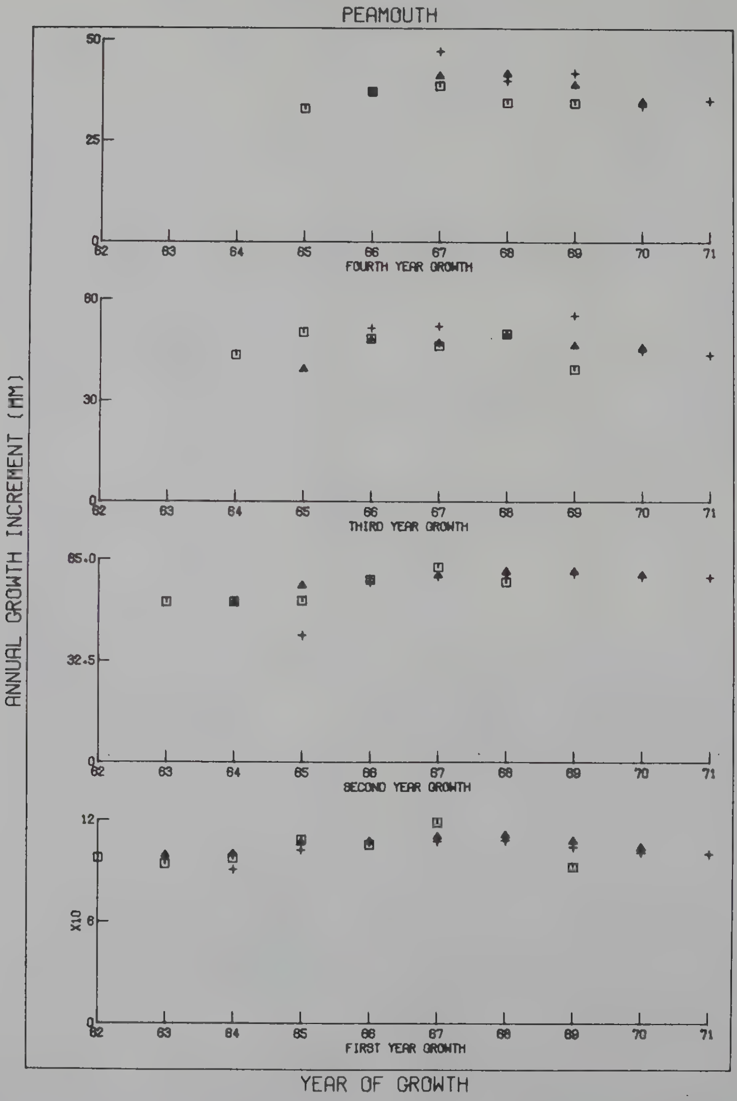

FIG. 8. Mean annual growth increments (mm) for each of the first four years of growth for peamouth caught in 1970 (□), 1971 (♠), and 1972 (+). The 1962–69 year-classes were sampled in 1970, the 1963–70 year-classes were sampled in 1971, and the 1964–71 year-classes were sampled in 1972. Data from Nishimoto (1973).

and Werner 1977) demonstrated substantial diet overlap among cohabiting fish species. However, these fish communities were highly differentiated according to habitat utilized and timing of feeding. In Lawrence Lake, co-occurring largemouth bass and bluegill sunfish utilized different sized prey (Werner et al. 1977), which

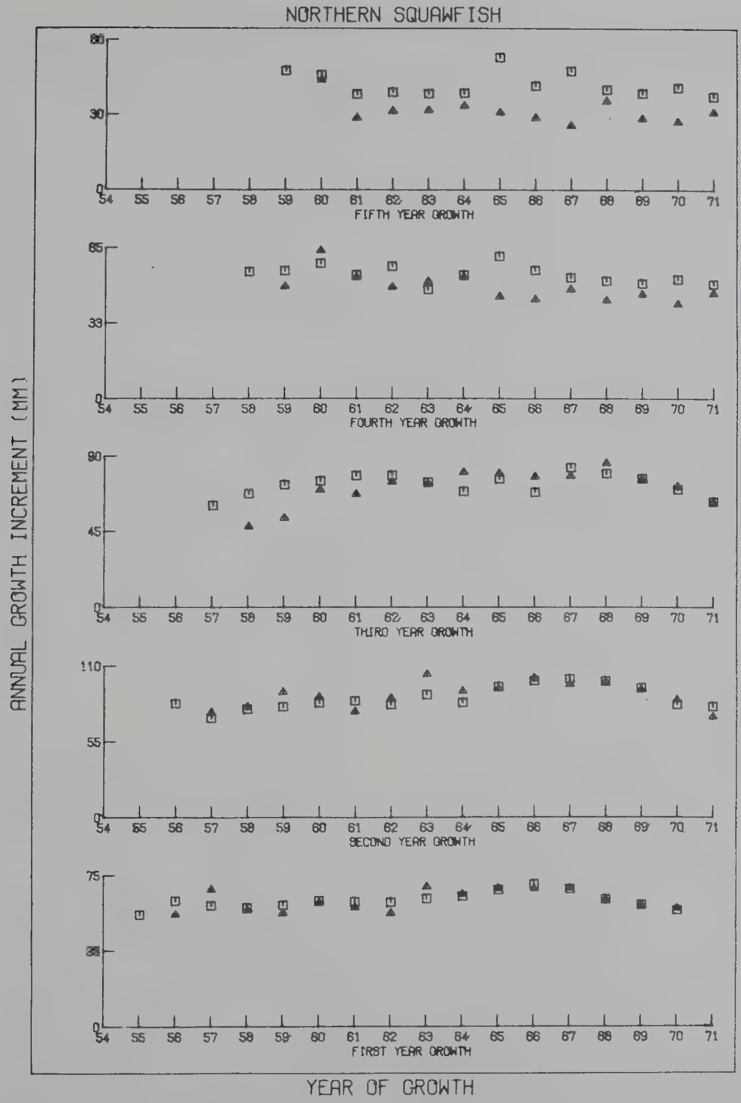

FIG. 9. Mean annual growth increments (length, mm) for each of the first 5 yr of growth (1954–72) for female (□) and male (▲) northern squawfish. Samples were collected 1971–73 for the 1955–70 year-classes. Data from Olney (1973).

reflected differences in functional morphology allowing bass to feed more efficiently on larger prey items (Werner 1977). These studies suggest that ecological segregation in fish communities is by habitat and reflects manifestation of competition.

Alternatively, it has been demonstrated that piscivorous fish predators can greatly affect the structure of fish communities. Introduction of peacock bass (*Cicla ocellaris*) in Lake Gatun, Panama, resulted in virtual extinction of the planktivorous fish population in wide areas of the lake (Zaret and Paine 1973). Introduction of largemouth bass into Lake Atitlan, Guatemala, resulted in similar destruction of the native fish populations (Dorris and Summerfelt 1968, cited in Paine and Zaret 1975).

Piscivorous fish predators have an important role in determining community structure of African lakes. In African lakes having the large piscivorous predators, tigerfish (*Hydrocyon vittatus*) and Nile perch (*Lates* sp.), small fish are restricted to areas with submerged vegetation or to very shallow areas where large predators cannot maneuver (Jackson 1961). Jackson speculated that the most common reproductive behaviors of fishes in African lakes (mouth brooding, the universal reproductive strategy among African ciclids, and anadromy, in which adults migrate to riverine spawning areas) are adaptations against piscivorous predation.

Lowe-McConnell (1975), in her monograph analyzing tropical freshwater fish communities, suggested that evolution in benthic–littoral and pelagic fish communities leads to two different ends that are largely explained by the different manifestations of piscivorous predation. Benthic–littoral fish communities are characterized by a large number of cohabiting fish species with complex trophic and habitat specializations. In the benthic–littoral environment, predation restricts fish to areas of cover, effectively preventing movement between habitats and acting as an isolation mechanism (Fryer 1959). Competition for resources within this habitat further increases diversity and trophic specialization.

Pelagic environments are characterized by a uniform prey resource of small individuals. There is no cover and the only effective refuge is behavioral — that is, remaining in areas of low light intensity, schooling, and feeding briefly (Eggers 1978). Piscivorous predation in the pelagic environment does not isolate populations, rather it forces a more or less uniform behavioral response. Pelagic fish communities are characterized by few species and uniform genotype (small body size necessary to exploit zooplankton) and feeding behavior.

Northern squawfish have significant impact on juvenile sockeye salmon, the most abundant planktivore of Lake Washington. To estimate the number of juvenile sockeye eaten by squawfish, monthly values of material ingested (see footnote 6 of Table 7) were transformed into number of fish by multiplying the ration (kilograms of carbon) by the proportion of sockeye in the squawfish, then dividing by the mean body carbon content of an individual sockeye, and summing over each month of the year. This estimate applies to June 1972–May 1973 or period of lacustrine residence for the 1971 year-class of sockeye salmon, which outmigrated in 1973.

During this period, northern squawfish consumed three million juvenile sockeye salmon. The expected seasonal abundance curve, assuming northern squawfish were the agents of all sockeye mortality, seems to be consistent with observed seasonal abundance (Traynor 1973). However, sockeye were a minor (10–30%) dietary item of northern squawfish and prickly sculpin the major item (70%). If sockeye were the major dietary item, squawfish could potentially consume 22 million sockeye.

Bryant (1976) showed that in years of high sockeye abundance, sockeye experienced much higher rates of mortality during their lacustrine residence than in years of low sockeye abundance. The abundance of juvenile sockeye from the 1971 year-class was much lower than earlier year-classes that experienced much greater mortality.

These observations suggest that northern squawfish feed heavily on sockeye when sockeye are abundant and switch to prickly sculpin (the most abundant and productive species in the lake) when sockeye abundance is low. Thus, predation by northern squawfish may be a compensatory process except at very high sockeye abundance (previously not observed in the lake).

Juvenile sockeye salmon show complex feeding behavior that seems to minimize vulnerability to predation by the visual piscivore, northern squawfish, while achieving energy requirements (Eggers 1978). Longfin smelt and threespine stickleback, also planktivores, show similar feeding behavior. Northern squawfish, because of their high biomass (Table 4) and respiratory requirements, hence high ration requirement, exert significant mortality on the planktivorous fish community in Lake Washington. To avoid predators, juvenile sockeye limit the time engaged in foraging and generally occur in regions of low light intensity that are removed from regions of high zooplankton abundance. Finally, sockeye engage in schooling behavior which reduces foraging efficiency (Eggers 1976) to minimize further risk of predation. The consequences of this antipredator behavior is that planktivores exploit only a part of the total zooplankton-containing habitat in the lake.

The available information, although not as well developed as information on planktivores, implies that piscivorous predation has a substantial impact on benthic–littoral fishes in Lake Washington. Mature benthic–littoral fishes exploit prey items much larger than zooplankton, and consequently have larger body sizes than planktivores. Their large body size effectively reduces piscivorous predation. However, larval and juvenile benthic–littoral fishes are extremely vulnerable to predators. In addition to northern squawfish, yellow perch and prickly sculpin commonly feed on larval and juvenile benthic–littoral fishes (Fig. 4). Thus, this group has more potential predators than do Lake Washington planktivores.

There are three types of reproductive strategies found in the Lake Washington fish community. The eggs of sockeye salmon and longfin smelt are deposited in the Cedar River. Young-of-the-year sockeye and smelt are limnetic upon entering the lake during the spring. Prickly sculpin construct nests in littoral and profundal areas of the lake (Rickard 1978) and young-of-the-year are epibenthic. All other major species — stickleback, peamouth, squawfish, yellow perch, and suckers — are substrate spawners in littoral regions (Scott and Crossman 1973). Their young-of-the-year occur in a narrow band near shore in exposed littoral zones with few macrophytes. In regions with macrophyte growth, the distribution of these young-of-the-year fish is more widespread (Dykeman 1978). Cover, shallowness, and low light intensity of these habitats provide effective refugia.

Werner et al. (1977) and Hall and Werner (1977) also showed similar patterns for small fish — shiners (*Notemigonus* sp. and *Notropis* sp.), and fry and juveniles of species that are large as adults — in Lawrence Lake. DiCostanzo (1957) found year-class strength of sunfish in some Iowa lakes positively correlated with amount and distribution of macrophyte growth.

Are the abundances of benthic–littoral fish species in Lake Washington limited by resources exploited by larval and juvenile forms within these littoral and epibenthic refugia, or by the resources exploited by the less vulnerable maturing and older juvenile community? It is not clear how fry and juvenile species cohabiting in available refugia can give rise to resource partitioning among older fish not vulnerable to predation. For this to occur, the number of fish surviving the refugia must be sufficient for the resulting population, not vulnerable to predation, to deplete resources outside the refugia. In this case resource depletion would limit reproductive potential and consequently limit the input of fry to available refugia below levels that would deplete resources of the refugia. Conversely, resource limitation in the refugia would weaken the competitive interaction of adult cohabiting species.

The recruitment to the adult benthic–littoral and northern squawfish population from refugia inhabited by larvae and juveniles of these species is probably sufficient for these forms to dominate the Lake Washington fish community.

The Lake Washington planktivorous fish community depends on recruitment from the Cedar River spawning area, and on the littoral refugia in the case of stickleback. However, recruitment from these areas has not been sufficient to swamp the squawfish population. Compensatory mortality of juvenile sockeye due to northern squawfish predation has offset positive population increases in years of good survival of eggs in the Cedar River. The limnetic environment offers limited refuge from piscivore predation.

One would expect the production of planktivorous fish to be low in a system like Lake Washington where the piscivores are relatively insensitive to planktivore abundance. This is because of the age structure of the squawfish population and availability of the abundant prickly sculpin as alternative prey.

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7811

Fate of ^{14}C-benzene in Eggs and Larvae of Pacific Herring (*Clupea harengus pallasi*)

MAXWELL B. ELDRIDGE, TINA ECHEVERRIA

Southwest Fisheries Center, Tiburon Laboratory, National Marine Fisheries Service,
National Oceanic and Atmospheric Administration, Tiburon, Calif. 94920, USA

AND SID KORN

Northwest and Alaska Fisheries Center, Auke Bay Fisheries Laboratory, National Marine
Fisheries Service, National Oceanic and Atmospheric Administration, Auke Bay,
Alaska 99821, USA

ELDRIDGE, M. B., T. ECHEVERRIA, AND S. KORN. 1978. Fate of ^{14}C-benzene in eggs and larvae of Pacific herring (*Clupea harengus pallasi*). J. Fish. Res. Board Can. 35: 861–865.

Eggs and larvae of Pacific herring were exposed to low concentrations of ^{14}C-labeled benzene, a soluble, aromatic component of crude oil. All life stages accumulated benzene from water in direct proportion to the initial exposure concentrations, reaching equilibrium within 6–12 h. Feeding larvae exposed to benzene through water and live food accumulated benzene initially from the water, then secondarily from the food. The maximum amount of benzene accumulated in tissues was inversely related to age. Eggs accumulated up to 10.9 times the initial concentration, yolk-sac larvae up to 6.9 times, and feeding larvae to 3.9 times. Reasons for these differences in total accumulation and uptake rate are discussed. Results provide evidence for food web magnification of petroleum-based hydrocarbons.

Key words: Pacific herring, *Clupea harengus pallasi*, eggs and larvae, ^{14}C-benzene, uptake, depuration, food chain, petroleum-based hydrocarbons

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Des oeufs et des larves de hareng du Pacifique furent exposés à de faibles concentrations de benzène, un constituant aromatique soluble du pétrole brut. marqué au ^{14}C. Tous les stades biologiques accumulent du benzène en provenance de l'eau en proportion directe des concentrations initiales d'exposition, jusqu'à ce qu'un équilibre s'établisse en dedans de 6 à 12 h. Des larves capables de se nourrir, exposées à du benzène à la fois dans l'eau et dans leur nourriture vivante, accumulent le benzène d'abord de l'eau, ensuite de la nourriture. La quantité maximale de benzène accumulée dans les tissus est en relation inverse de l'âge. Les oeufs accumulent jusqu'à 10.9 fois la concentration initiale, les larves vésiculées jusqu'à 6.9 fois et les larves qui se nourrissent jusqu'à 3.9 fois. Nous analysons les raisons de ces différences dans l'accumulation totale et le taux d'assimilation. Ces résultats sont une preuve de l'accroissement, dans le réseau alimentaire, des hydrocarbures du pétrole.

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NUMEROUS researchers have shown that marine organisms representing different species and trophic levels take up and release petroleum hydrocarbons (Lee et al. 1972; Teal and Stegeman 1973; Vaughan 1973; Anderson et al. 1974; Fossato 1975; Lee 1975; Corner et al. 1976; Korn et al. 1976). In radiometric studies marine organisms more rapidly metabolized *n*-alkanes than aromatics (Lee 1975).

Studies of the relatively more toxic aromatic fractions have concentrated on the higher aromatics and only lately have investigators examined benzene, a relatively abundant (up to 6.75 mg/L in the water-soluble fraction) and soluble aromatic (1993 μL/L) component of crude oil (Anderson et al. 1974; Benville and Korn 1974). Benzene at concentrations of 20–45 μL/L is acutely toxic and at 5–10 μL/L is chronically toxic to Pacific herring (*Clupea harengus pallasi*) eggs and larvae (Struhsaker et al. 1974) and at 2–11 μL/L is acutely toxic to various juvenile and adult fishes (Meyerhoff 1975; Benville and Korn 1977). Korn et al. (1976, 1977) and Roubal et al. (1977) found that in juvenile and adult fishes aqueous benzene rapidly entered the fish and was metabolized in the liver. In nearly all studies

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TABLE 1. Summary of experimental variables for ^{14}C-benzene uptake and depuration tests with Pacific herring embryos and larvae. All tissues were sampled at 6, 12, 24, 48, and 72 h except marked (*) treatments, which ended at 48 h.

Life stage	Type of exposure	Initial mean benzene concn (μL/L)	Specific activity (cpm/nL)	Total wet wt (mg)		Estimated no. of individuals per sample
				mean	±SD	
Egg—embryo	Benzene-treated water	0.063	20.00	158.9	±21.3	81
		0.560	2.00	155.3	±16.0	79
Yolk-sac larva	Benzene-treated water	0.036	13.00	147.2	±56.2	118
		0.460	0.90	127.9	±46.6	102
Postyolk-sac larva	Benzene-treated water	0.144	2.20	154.5	±35.5	144
		1.200*	5.00	135.1	±36.1	126
		2.100	0.14	170.4	±40.4	158
	Benzene-treated food and clean water	1.200*	5.00	117.5	±25.6	109
	Benzene-treated water and clean food	1.440*	2.20	149.7	±70.1	139
		2.100	0.14	148.8	±65.7	138
	Benzene-treated food and water	1.200*	5.00	129.2	±43.1	120

juvenile and/or adult life stages were used, and they were only exposed to hydrocarbons in the water.

The object of this study was to determine the fate of benzene in the eggs, yolk-sac larvae, and feeding larvae of Pacific herring. We wished to compare the uptake of benzene from the water with that from food and determine whether biomagnification occurred, as has been demonstrated with pesticides (Hickey and Keith 1965; Woodwell et al. 1967; Macek and Korn 1970; Reinert 1972).

Materials and Methods

TEST ANIMALS

For experiments with eggs, Pacific herring (*Clupea harengus pallasi*) eggs were artificially fertilized with gametes of freshly caught, sexually mature adults. A single layer of eggs was spread over 10 × 24 cm glass plates and placed in green polyethylene-plastic rectangular pans filled with 8 L of filtered (pore size 2 μm) seawater. In the experiments with larvae, naturally fertilized eggs were gathered in San Francisco Bay and incubated in similar pans. After hatching, larvae were transferred to new pans filled with freshly filtered seawater.

Postyolk-sac feeding larvae (9.4 mm mean standard length) were fed marine rotifers (*Brachionus plicatilis*) which were cultured according to the techniques of Theilacker and McMaster (1971), except that the small green flagellate (*Nephroselmis* sp.) was used as rotifer food. Rotifer concentrations were maintained at 14–20 rotifers/mL as determined with a Model ZBI Coulter counter.

EXPERIMENTAL CONDITIONS

Experiments were conducted in the previously described 8-L pans, under static conditions. Freshly filtered seawater was added at the beginning of each experiment, and temperature, dissolved oxygen, and salinity were measured daily. To stabilize water conditions pans were held in water baths under constant light (about 1900 lx). Dissolved oxygen values were at or near saturation, salinities were constant at 23.0‰, and temperature ranged from 12.2 to 13.5°C throughout the experiments.

EXPOSURE PROCEDURES

Animals were given a single dose of benzene just after fertilization, just after hatching (yolk-sac larvae), and at completion of yolk absorption (feeding larvae). They were therefore exposed to continuously declining concentrations of benzene, which from previous experiments has been shown to decline exponentially to ~25–30% of the initial concentration within 24 h (Struhsaker et al. 1974). Aqueous benzene was introduced directly into the water in the form of benzene-saturated seawater (1 mL benzene to 250 mL seawater vigorously shaken and settled for 1 h). Ring-labeled ^{14}C-benzene of the desired specific activity (Table 1) was added to this stock solution and the appropriate amount of benzene added to the test containers. An attempt was made to introduce benzene in two concentrations of 1.00 and 0.10 μL/L. Due to its volatility and the difficulty in dissolving benzene, the actual in situ concentrations of benzene ranged from 0.010 to 2.100 μL/L as determined by gas chromatography (Table 1). In the feeding larval experiment ^{14}C-labeled benzene was introduced in three ways: (a) in contaminated water only, without food, (b) in benzene-contaminated rotifers only, and (c) in benzene-contaminated water and benzene-contaminated rotifers.

We contaminated the rotifers by introducing ^{14}C-labeled benzene to the rotifer rearing container at ~0.1 and 1.0 μL/L concentrations. The rotifers were allowed to accumulate benzene for 2 d. They were then removed, rinsed with fresh seawater, and fed to the larvae.

WATER AND TISSUE ANALYSES

Two water and tissue samples were taken at 6-, 12-, 24-, 48-, and 72-h intervals. The 1-mL water samples were added to 10 mL Instagel scintillator and counted in a Packard Tri Carb scintillation spectrometer. For tissue samples live larvae were rinsed with distilled water, weighed (Table 1), placed in a vial with solubilizing solution (1 mL/100 mg tissue Packard Soluene-100) for 48 h and combined with 10 mL of scintillator (Packard Dimilume). To avoid rapid drying of the samples and the potential loss of benzene we

TABLE 2. Decreasing concentrations (μL/L) over 48 h of ^{14}C-labeled benzene in the water of experiments with Pacific herring eggs and larvae.

Expt	Life stage	Hours					% volatilized at 24 h
		0	6	12	24	48	
1	Embryo	0.063	0.007	0.007	0.003	—[a]	60
1	Embryo	0.560	0.035	0.029	0.023	—	77
2	Yolk-sac larva	0.036	0.023	0.020	0.018	—	50
2	Yolk-sac larva	0.460	0.356	0.329	0.205	—	55
3	Postyolk-sac larva	0.144	0.088	—	0.056	—	61
3	Postyolk-sac larva	2.100	1.320	—	0.723	—	68
4	Postyolk-sac larva	1.200	0.800	0.580	0.360	—	60

[a] No detectable concentration.

did not count the numbers of individuals in each sample. Rather, we estimated their numbers (Table 1) by using Ehrlich's (1972) determinations of water content and our own dry weight measurements. Method efficiency was 61%, predetermined with spiked samples of known counts per minute (cpm). Water and tissue samples with emissions below 40 cpm were considered below the detectable limits of our system.

Radiometric analysis measures ^{14}C and cannot determine if the label remains on an intact benzene ring or on a metabolite of benzene. Since we did not analyze for the presence of benzene metabolites, all results and discussion on accumulation and depuration must be considered to represent benzene and/or benzene metabolites.

Results and Discussion

Aqueous benzene concentrations in our test containers decreased exponentially in the first 24 h after introduction (Table 2) as was found in previous larval fish experiments (Struhsaker et al. 1974); benzene was absent after 48 h.

Embryos and yolk-sac larvae responded to single exposures of aqueous benzene in almost identical fashion. Both rapidly accumulated benzene to maximum levels within 6–12 h after exposure (Table 3). Embryos then lost benzene at an exponential rate, declining to levels just above the initial exposure concentrations. Yolk-sac larvae began depurating between 24 and 48 h but differed from embryos by exhibiting an increase in ^{14}C-benzene between 48 and 72 h. How yolk-sac larvae accumulated benzene after a period of depuration is difficult to explain, since free benzene was not detectable in the water. However, fish larvae are known to increase their tissue water content when starved (Ehrlich 1974). Until feeding is well established some tissue resorption takes place, a condition which, if continued, would lead to starvation and eventual death. Benzene may enter larvae via infused water.

Like embryos and yolk-sac larvae, nonfeeding postyolk-sac larvae exposed to three aqueous concentrations (0.144, 1.200, and 2.100 μL/L) quickly absorbed benzene, attaining maximum accumulations within 6–12 h (Table 3). Subsequent depuration followed with leveling off at or near the original exposure concentrations.

Postyolk-sac larvae feeding on contaminated rotifers or rotifers in contaminated water demonstrated a bimodal uptake response to benzene exposure. When benzene in situ concentrations of 0.140 and 2.100 μL/g were added to water containing larvae actively feeding on clean rotifers, larvae rapidly accumulated benzene during the first 6 h (Table 3). This initial accumulation was similar to the previously described response of unfed larvae and presumably represents uptake of aqueous benzene. Depuration from larval tissues between 6 and 24 h was slow or nonexistent, and after this period uptake was again exhibited. Maximum concentrations of 0.49 and 8.160 μL/g were reached at 48 and 72 h for the low and high exposure concentrations, respectively. Larvae apparently ingested rotifers during this latter period which had become contaminated from the aqueous benzene. In a separate treatment larvae exposed to both contaminated water and precontaminated rotifers responded the same as larvae exposed to benzene-contaminated water only and clean rotifers (the 0.140 and 2.100 μL/L of Table 3). The initial benzene accumulation in the doubly exposed larvae reached 2.47 and the second buildup reached 3.98 μL/L. In the final treatment, larvae that fed on only rotifers previously contaminated with 1.200 μL/L benzene experienced no initial rapid accumulation; rather a steady rise in contamination to 0.310 μL/L was exhibited.

The secondary accumulation of benzene by ingestion of rotifers appeared to be a lower but potentially more accumulative process. The principal reason for this is that *B. plicatilis* appears incapable of either discharging or metabolizing benzene for time periods far exceeding the developmental period when herring larvae would depend on them for food (Echeverria unpublished data). In experiments conducted at our laboratory we found rotifers accumulated and retained benzene and/or its metabolites 10^3–10^4 times the original concentration for periods up to 8 d. Larvae fed on rotifers that in turn were accumulating higher concentrations of ^{14}C hydrocarbons. The longer time period needed for rotifers to

TABLE 3. Means ±SE of benzene concentrations (nL/g) in exposed Pacific herring eggs and larvae.

Life stage	Initial exposure concn (μL/L)	Hours				
		6	12	24	48	72
Embryo	0.063	0.58±0.04	0.61±0.01	0.32±0.02	0.18±0.01	0.10±0.00
	0.560	6.10±0.30	6.14±0.19	3.45±0.14	1.26±0.02	0.91±0.00[a]
Yolk-sac larva	0.036	0.25±0.01	0.13±0.02	0.09±0.01	0.10±0.00	0.39±0.01
	0.460	2.40±0.15	3.12±0.19	1.81±0.10	0.67±0.02	0.89±0.02
Unfed larva	0.144	0.22±0.02	0.23±0.02	0.17±0.01	0.18±0.03	0.17±0.00[a]
	1.200	3.21±0.00[a]	3.10±0.09	1.44±0.09	1.24±0.21	—
	2.100	4.09±0.09	4.06±0.09	2.84±0.19	2.78±0.02	2.74±0.05
Fed larva	0.140	0.23±0.01	0.25±0.01	0.26±0.00	0.49±0.07	—
	1.200	0.04±0.01	0.10±0.05	0.22±0.07	0.31±0.04	—
	1.200	2.47±0.04	2.28±0.04	1.78±0.04	3.98±0.00[a]	—
	2.100	4.99±0.04	4.23±0.03	3.27±0.05	6.22±0.12	8.16±0.15

[a] Only one sample used for calculation.

take up and concentrate these hydrocarbons explains the secondary or delayed response in herring uptake. The presence of aqueous benzene seems to affect the amount of benzene taken up by rotifers and hence by larvae. When contaminated rotifers alone were present, larvae accumulated only 0.3 μL/L of the original concentration. Further sampling beyond 48 h is needed to determine whether larvae would continue to accumulate benzene. In a simple comparison between results (Table 3), we calculated the relative contribution of benzene derived from the water versus from the food. In the first rapid uptake an average of 91% of tissue benzene was obtained from the water. The second peak at 48 h was an average of 38% from the water and 62% from rotifers. Presumably larvae would proportionally take up more benzene from rotifers in time as waterborne benzene concentrations declined and rotifers accumulated more.

The maximum amount of benzene accumulated in tissues differed among early life stages. The younger the stage, the higher the concentration factor. Eggs absorbed benzene 9.7 and 10.9 times the concentrations added to the water, and yolk-sac larvae accumulated 6.9 and 6.8 times the initial concentration. After yolk absorption, larvae accumulated less benzene than either eggs or yolk-sac larvae. Factors ranged from 0.3 for larvae feeding on precontaminated rotifers to 3.9 times the initial exposure concentration in larvae feeding on rotifers in benzene-contaminated water. This highest accumulation of benzene occurred 72 h after exposure (Table 3) when larvae were feeding on rotifers and there was no indication of a decrease in accumulation. The uptake patterns seen in the accumulations of other postyolk-sac larvae fed rotifers (Table 3) also suggest maximum levels had not been reached. No samples were taken after 72 h.

All stages accumulated benzene rapidly from the water, but those with yolk exhibited higher tissue magnification factors than larvae past the stage of yolk absorption. Higher concentration factors in these yolk-containing stages are most likely caused by two factors: the high lipid content of yolk-bearing stages and the lack of specialized tissues. Korn et al. (1976) found benzene accumulated predominantly in tissues with high lipid content in teleosts. Lipophilic benzene probably accumulated in the lipid-rich yolk of the herring eggs and yolk-sac larvae. The content of lipids in conspecific Atlantic herring (*Clupea harengus harengus*) eggs has been determined by Ehrlich (1972) to be 18.12% of egg dry weight. In related experiments we measured oxygen consumption which showed herring larvae had much higher metabolic rates than eggs. This would mean utilization of lipid-rich yolk and excretion rates would be less in embryos than in active larvae, thereby affecting the turnover rate of benzene in the two life stages.

It is commonly believed the liver is a major site of petroleum hydrocarbon metabolism. Livers and gallbladders of adult fishes have been found to accumulate the highest concentrations of benzene over all tissues tested (Korn et al. 1976; Roubal et al. 1977). The metabolism and/or depuration of benzene is likely slower in the less-developed life stages lacking these functional organs.

Until recently no evidence existed for food-web magnification of petroleum-based hydrocarbons (Lu and Metcalf 1975; National Academy of Sciences 1975; Koons et al. 1976). Corner et al. (1976), however, found that *Calanus helgolandicus* responded to naphthalene exposure in much the same manner as did herring larvae. Hydrocarbons accumulated through the diet were quantitatively more important than those taken up directly from solution. Accumulation and depuration of hydrocarbons were much slower when obtained from contaminated food. Results of our study clearly demonstrated that fish larvae feeding on zooplankters that cannot metabolize or discharge petroleum hydrocarbons in short time periods do accumulate hydrocarbons to amounts in excess of the exposure concentrations. Further, zooplankters of this type or copepods with high hydrocarbon contents provide a pathway of entry for petroleum hydrocarbons that may be more significant than through the water.

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7812

ROLE OF THE OIL GLOBULE IN SURVIVAL AND GROWTH OF STRIPED BASS (*Morone saxatilis*) LARVAE

by Maxwell B. Eldridge, Dennis J. King, Dana Eng, and Michael J. Bowers

National Marine Fisheries Service
Southwest Fisheries Center - Tiburon Laboratory
3150 Paradise Drive
Tiburon, California 94920

Introduction

After years of studying the striped bass (*Morone saxatilis*) population in the Sacramento-San Joaquin Estuary it was recently concluded that the number of bass entering the fishery is largely a function of survival during the early life stages (Stevens, 1977). Although they found survival was positively correlated with river flows, the direct causative factors which affect egg and larval mortality have not been determined. At the National Marine Fisheries Service, Tiburon Laboratory, we have been working with the assistance of the California Department of Fish and Game on experiments to determine how different inherent and environmental variables affect survival, growth and development in striped bass eggs and larvae. In the course of these experiments we noticed the vital role the oil globule played in allowing feeding larvae to adapt to stresses. In this paper we present results which show how striped bass larvae depend on the energy rich oil globule to meet metabolic requirements under various food densities.

Methods and Materials

Eggs artificially fertilized by a single striped bass male were obtained from the California Dept. of Fish and Game Central Valleys Hatchery at Elk Grove, California during the 1976 and 1977 spawning season. After water hardening, eggs were transported in styrofoam containers to the Tiburon Laboratory and incubated at 18° C in glass McDonald jars. Larvae hatched approximately 48 hours after fertilization and were allowed to collect in a 50-gallon fiberglass tank. The fourth day after fertilization larvae were transferred to green acrylic plastic containers shaped like 1/2 spheres. Containers used for subsampling of larvae were stocked with 150 larvae per pan. Containers used for measuring survival were stocked with 25 larvae per pan. Two replicates for subsampling and two for survival were filled for each food concentration. Larvae were fed *Artemia salina* in 3 densities of 6.2, 4.0 and 2.2 per ml, hereafter referred to as high, medium and low concentrations. These fed larvae were compared to unfed larvae in subsequent measurements. Temperature, pH, and dissolved oxygen were measured daily (Table 1). Salinity was maintained at 3.0 ppt from hatching until day 9 at which time it was increased to 10.5 ppt. Water and food were changed on alternate days. Survival was determined daily by making 3 replicate visual counts in each pan. Preliminary point-of-no-return experiments were run in which 2 pans with 25 larvae each were starved for one week and fed. Two more pans with 25 larvae each were starved for 2 weeks, then fed. Samples of 5 to 10 larvae were taken daily for measurements of growth and development, the specimens being anesthetized first with ms 222 and preserved. The oil globule in each egg and larvae was measured for volume (ellipsoid volume $= (\pi LH^2)/6$) with an ocular micrometer in a dissecting microscope. One half of each day's specimens of each treatment was dissected to remove the oil globule and food from the gut. We removed only food from the guts of remaining larvae and left the oil globule intact. Both sets of specimens were dried at 66°C for 24 hours and weighed on a Cahn electrobalance to the nearest microgram. Dry weights of the oil globules were obtained by subtracting the average dry weight values of the dissected larvae from those of the intact larvae. Tissue weights were represented by larvae with the oil and food removed.

Caloric contents of oil, tissue and whole eggs were determined with a Parr adiabatic calorimeter. Oil was extracted and concentrated by means of a freon solvent extraction. Tissue samples were taken from larvae which had completed total oil consumption.

Percent dry weight composition of the lipid fraction in freshly spawned eggs was calculated by a 2:1 chloroform/methanol extraction in a micro-Sohxlet extractor. Results were checked by using heptane as a solvent and less than 1% variation was obtained. The chemical content of the extract was analyzed by NMR (Nuclear Magnetic Resonance) analysis at the California State University, San Francisco.

Results - (35 mm colored and black and white photomicrographs accompany this section illustrating growth and development of the embryo and larva and the progressive consumption of the oil globule.)

Description -

Maturation of the ovum prior to fertilization is characterized by a coalescence of many oil globules into a single large globule (Bonn et al, 1976; Mansueti, 1958). The dominant features of the relatively large, (average diameter of 3.4 mm), pelagic egg are the chorion, large perivitelline space, yolk and oil globule. Eggs averaged 280 micrograms (μg) in total weight. Estimates of the percent dry weight composition of the oil globule differed according to the solvent used for extraction. Freon extraction estimates of two females from 1976 were 56.8 and 38.0% (2 replicates/female). Chloroform / methanol (2:1) extraction of a third female from 1977 showed 63.4% (4 replicates).

The varying amounts of oil in eggs from different females resulted in different caloric contents per unit weight of eggs, 8323 and 7816 cals/gm. Eggs averaged 2.21 calories per egg, higher than most other fish species. This original egg energy consisted of 1.38 oil calories and 0.83 yolk calories. Oil was found to be a high energy source with 9291 cals/gm.

In recent (1977 season) tests of the chemical content of the oil it was found by NMR analysis to consist primarily of tryglycerides. This agrees with descriptions of oil globules in other fish eggs (Smith, 1957).

Utilization of the Oil Globule -

Prior to feeding the embryo and yolksac larva rely solely on endogenous energy sources--those contained in the yolk and oil globule. We found the yolk was consumed first. Total yolk consumption coincided with the onset of feeding, 7 days after fertilization, 5 days after hatching. The oil globule, however, remained approximately the same in size and weight until this time.

The rate of oil globule consumption was markedly different between fed and starved larvae (Figures 1, 2 and 3). Starved larvae conserved their oil globule as shown in the volume dry weight determinations and did not grow or develop at all until their deaths. In contrast fed larvae consumed their oil in nearly identical patterns. As larvae fed, they grew in direct relation to the food available (Figure 2). The only effect of food concentration on oil consumption in larvae was at the low concentration. These larvae contained oil for a longer period (up to day 27). The high density larvae had no oil after day 18. Experiments this year in which we exposed larvae to a wider range of food concentrations appear to consume oil in inverse proportion to the food concentration. Complete results of these experiments are still being analyzed.

Survival -

Larval survival began to decline (Figures 4 and 5) once larvae relied on either oil alone (as in the starved condition) or on oil and food combined to meet metabolic requirements. The highest mortality rates occurred as total oil consumption approached (days 14 to 22). At the end of the experiment on day 29, the percent surviving was directly related to the amount of food. The more food available the higher was the larval survival rate. Starved larvae survived to day 29 in the 1976 experiments and in the current 1977 experiments starved larvae were still alive after 34 days.

The point-of-no-return, the irreversible time at which starved larvae are unable to feed if food is presented, was never reached. Larvae starved one week and fed survived at 57% by day 29 and those starved two weeks survived 24%.

Discussion

The presence of oil globules in fish eggs and larvae is ecologically and phylogenetically widespread (see Russell, 1977 for marine fish examples). Some fishes have numerous droplets as *Solea solea* and *Trachinus vipera* while others like the striped bass have a single large globule. Although present in many other fishes nowhere in the literature have we found it in such large amounts. One problem is there are few papers describing the chemical composition of fish eggs. For comparison *Salmo gairdneri* (*irideus*) had 10.7% of its egg dry weight in oil (Hartman et al, 1947) and California sardine (*Sardinops caerulea*) eggs were found to have 13.0% (Lasker, 1962). The oil globule was first thought to have an important role in flotation (Cunningham, 1889). This was soon disproved when eggs without oil globules were found to have similar specific gravities (Russell, 1976). It is our conclusion that the oil globule serves a role of providing a high energy source in a compact form. The caloric content of oil was found to be much higher than that of yolk, 9291 versus 6917 calories/gm. In this way larvae have a large amount of energy available to meet metabolic needs in a form which does not require a large volume.

Utilization of the oil, which is characterized as mainly carotenoid-pigmented glyceride fats, is usually last (Smith, 1957; Blaxter, 1969). Proteinaceous yolk was consumed prior to feeding. This shows a more efficient use of the animal's resources since the yolk energy contains less energy per unit volume and weight.

Feeding larvae consumed their oil globule at faster rates than did starved larvae (Figures 1, 2 and 3). Evidently starved larvae were able to metabolically adjust to the absence of food, thereby conserving the only energy source available to them. Starved larvae did not grow during the experimental period of 29 days. Once food was given, however, as we found in the point-of-no-return experiments, the larvae proceeded to grow at normal rates.

Results of the point-of-no-return experiments and the long survival of starved larvae up to 29 days reveal a metabolic flexibility within striped bass larvae which has high survival value. This is especially important when one considers that striped bass larvae use estuaries as nursery grounds. These are generally ecosystems with highly variable environments. The oil globule provides the larvae with a reserve energy source upon which the animal can rely when food supplies are insufficient.

Table 1. Mean and range values of physical/chemical conditions in striped bass larval feeding experiments

	Mean	Range
Temperature	18.4	16.9 - 19.4
Dissolved oxygen	8.4	7.7 - 9.1
pH	7.8	6.9 - 8.2

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List of Figures

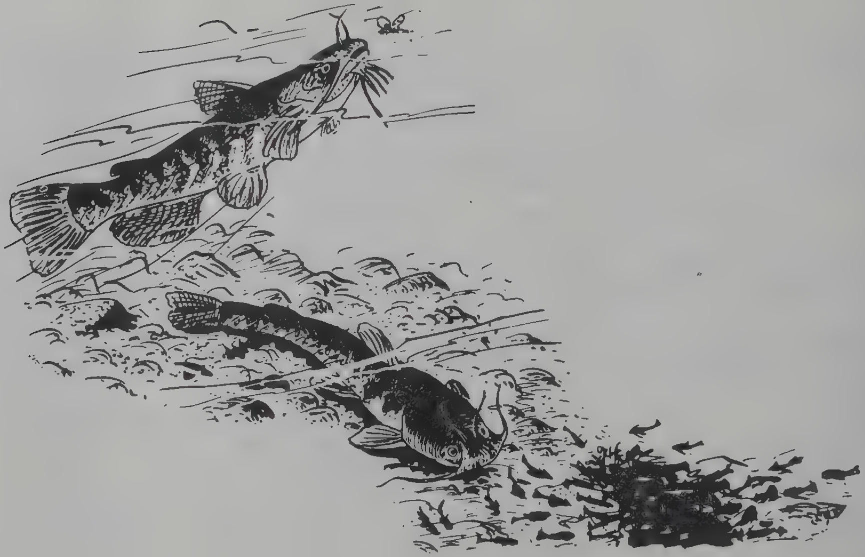
Figure 1. Dry weights (mg) of tissue and oil globules of striped bass larvae starved for 25 days.

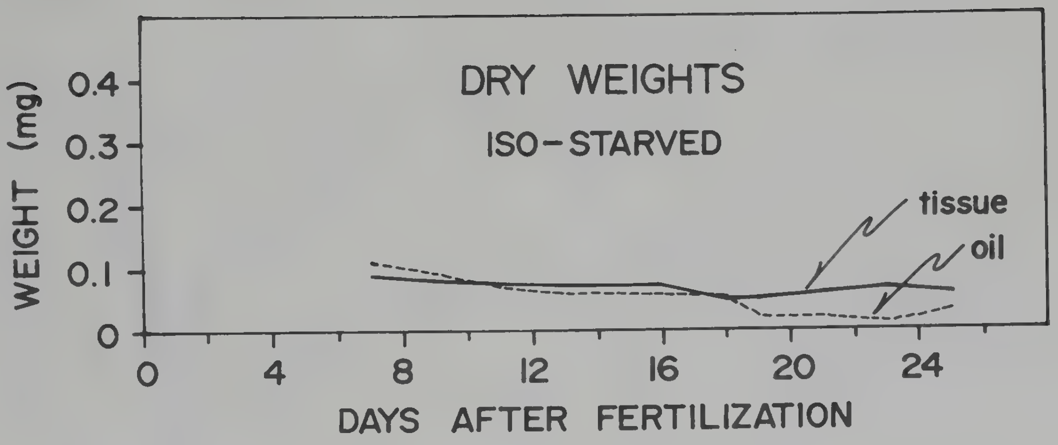
Figure 2. Dry weights (mg) of tissue and oil globules of striped bass larvae fed Artemia salina in 3 different concentrations.

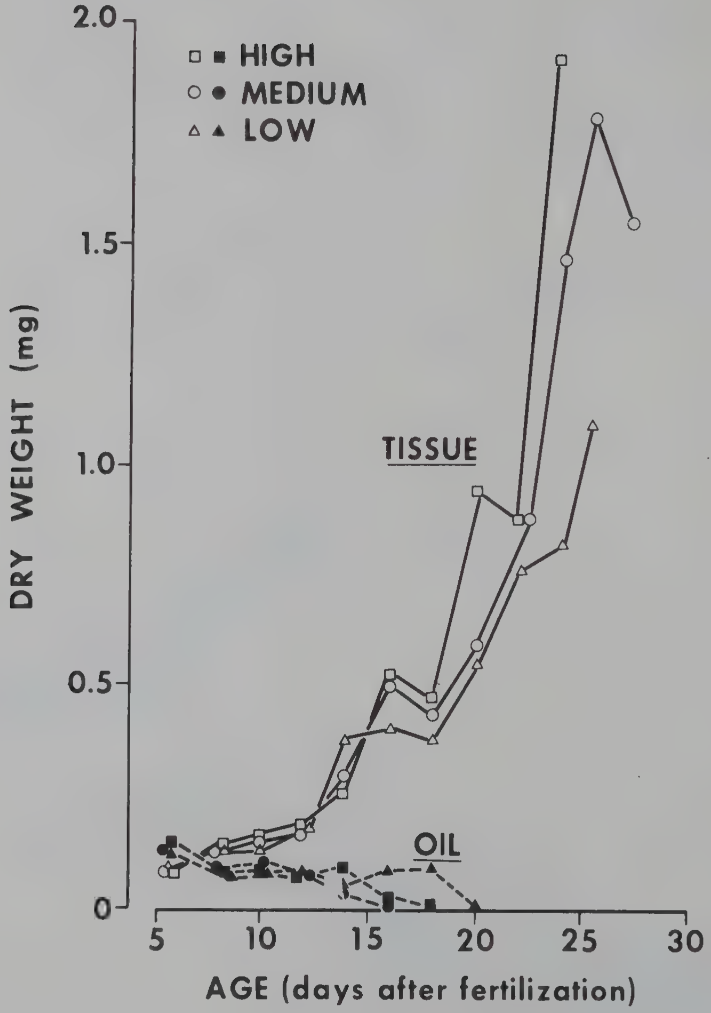
Figure 3. Oil globule volumes (mm^3) of striped bass larvae reared in 3 different concentrations of Artemia salina and starved.

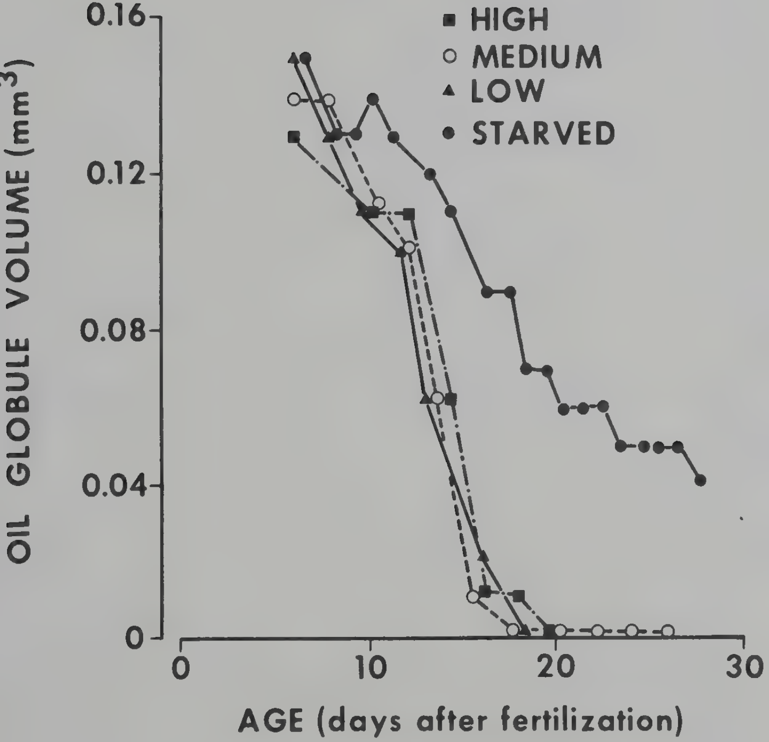
Figure 4. Mean percent survival of starved striped bass larvae reared for 29 days after fertilization.

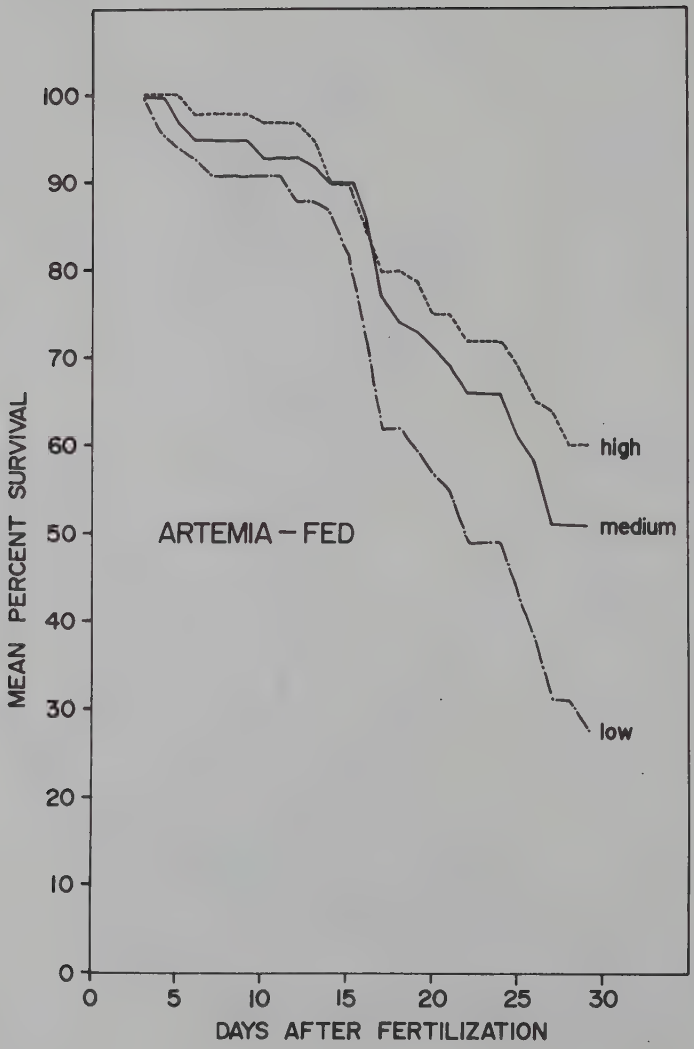
Figure 5. Mean percent survival of striped bass larvae fed 3 different concentrations of Artemia salina for 29 days.

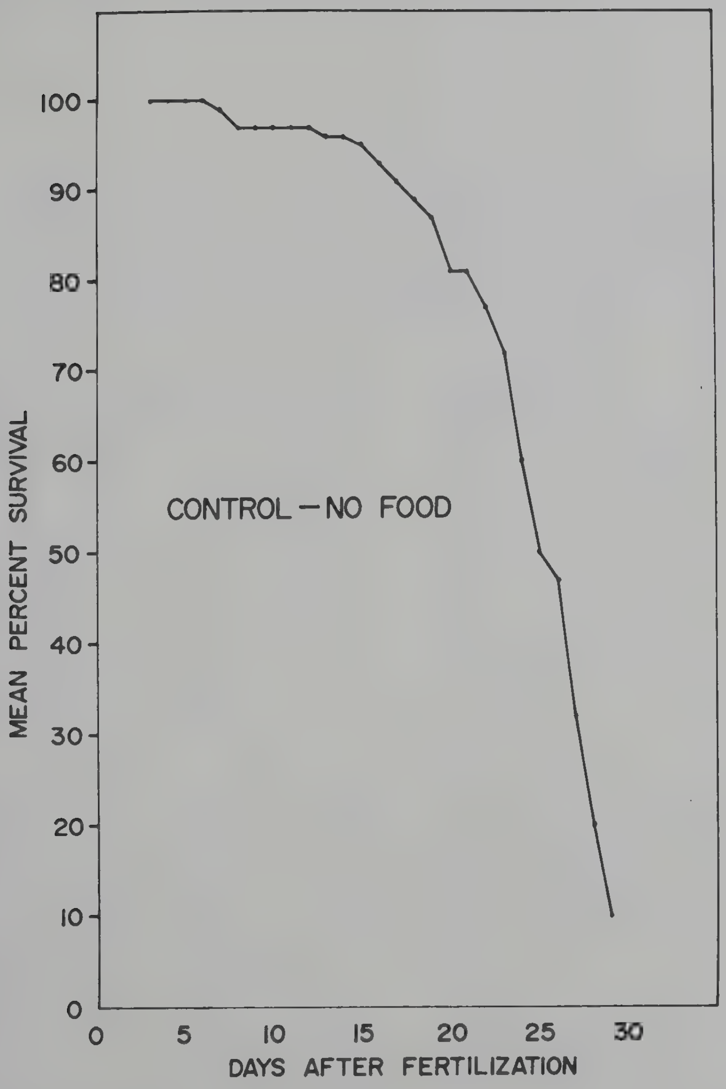


DRY WEIGHTS
ISO-STARVED
tissue
oil
WEIGHT (mg)
0.4
0.3
0.2
0.1
0
0
4
8
12
16
20
24
DAYS AFTER FERTILIZATION


□ ■ HIGH
○ ● MEDIUM
△ ▲ LOW
TISSUE
OIL
DRY WEIGHT (mg)
2.0
1.5
1.0
0.5
0
5
10
15
20
25
30
AGE (days after fertilization)


OIL GLOBULE VOLUME (mm^3)
0.16
0.12
0.08
0.04
0
AGE (days after fertilization)
0
10
20
30
■ HIGH
○ MEDIUM
▲ LOW
● STARVED


MEAN PERCENT SURVIVAL
0
10
20
30
40
50
60
70
80
90
100
DAYS AFTER FERTILIZATION
0
5
10
15
20
25
30
ARTEMIA – FED
high
medium
low


CONTROL — NO FOOD
MEAN PERCENT SURVIVAL
0
10
20
30
40
50
60
70
80
90
100
0
5
10
15
20
25
30
DAYS AFTER FERTILIZATION

7813

THE PRECISION OF SIMULATED TRANSECT SURVEYS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, SCHOOL GROUPS

PAUL C. FIEDLER[1]

ABSTRACT

Simulated transect surveys of model anchovy populations were compared in terms of precision and efficiency. The precision of systematic surveys varies inversely with the distance between transects. Systematic surveys give more precise population estimates than random surveys, due to the large positive correlation between closely spaced transects. The precision of stratified systematic surveys is not significantly different from that of the unstratified surveys when the school groups are randomly distributed in the survey area. However, stratified systematic surveys are more precise when the school groups are clumped in one end of the survey area. The results of the simulations show that the patchy distribution of anchovy schools can be a major source of error in population estimates.

Any sampling program intended to estimate the size of a population is subject to a variety of errors which may reduce the accuracy or precision of the estimate. Precision is the reciprocal of the variation of replicate estimates. Successful management of a northern anchovy fishery in California will require the monitoring of changes in the population size. Acoustic survey techniques are currently being developed to obtain population and biomass estimates independent of the fishery (Hewitt et al. 1976). As in the study of any biological population, it will be important to avoid confusing the variation of a series of estimates due to sampling error with true fluctuations in the population size.

Precision may be affected by 1) the manner in which the sampled population is distributed in space, and 2) variations within the sampling method itself. Several studies have shown that the patchy distribution of individuals in a population may cause considerable variation in replicate population estimates and that the variation is related to sample design. Winsor and Clarke (1940) studied the variation of catches in series of plankton net tows. Although they did not separate the components of between-tow variation due to factors (1) and (2), it was observed that oblique tows were more precise than vertical or horizontal tows. Barnes and Marshall (1951) took an extensive series of replicate pump samples and attributed the considerable variation observed to the nonrandom distribution of the zooplankton since the volumes filtered were known accurately. Taft (1960) analyzed the variance of sardine egg counts in a grid of closely spaced stations. The distribution of eggs was extremely patchy (the densities between samples ranged over more than four orders of magnitude) and the relative 95% confidence limits for an estimate of the egg population in the area of the grid from a single sample were represented by a factor of 62. A simulation study by Wiebe (1971) showed that the precision of zooplankton population estimates depends both on the sampling design (net size and tow length) and the distribution of the population (size and location of patches).

Similar studies have investigated the precision of sampling fish populations. Taylor (1953) discussed the implications of the patchy distribution of fish for the optimum design of trawl surveys to estimate population size. Cram and Hampton (1976) demonstrated that the patchy distribution of pilchard schools can cause imprecision sufficient to render a population estimate useless for management.

The anchovy population is patchy on two levels: individual fish are aggregated in schools and schools themselves tend to be aggregated in school groups. This patchiness, or nonrandomness, is expected to be a major source of variation in population estimates. The present study simulated surveys of model anchovy populations to determine the effect of patchiness on the precision of population estimates. Three transect survey designs were compared: systematic, random, and stratified systematic. These are merely different

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[1] Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093.

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methods of selecting transects, or allocating sampling effort. The three types of simulated survey, with a range of sample sizes (numbers of transects), were run on 15 model anchovy populations.

METHODS

Anchovy populations were modeled as arrays with each element representing 1 n.mi.^{2}. The array dimensions were 180 × 75, approximately the dimensions, in miles, of the Los Angeles Bight. Since a school is the population unit detected in an acoustic or aerial survey, the units of the model populations were schools. One hundred fifty thousand schools were distributed in the array resulting in a mean density of 11.1 schools mi^2. Four acoustic surveys by the California Department of Fish and Game[2] in 1975 and 1976 yielded estimates ranging from 88,887 to 319,878 anchovy schools off southern California in the area of the bight. Mais (1974) gave a range of 21,920-343,070 ($\bar{x}$ = 150,996) schools off southern California and northern Baja California, most of which were within the bight.

The schools were placed in circular school groups located at random. Schools were distributed uniformly within a school group. School group radii and densities were chosen randomly and independently from log-normal approximations of observed frequency distributions based on 52 school groups from six California Department of Fish and Game Sea Survey acoustic surveys (MacCall et al.[3]) (Figure 1). There was no significant correlation between the density of schools within a school group and the size of the school group in these observations. Where school groups overlapped, the densities were simply added together, although this effectively increased both the mean radius and density. In one model population illustrated in Figure 2, 16 school groups containing 150,303 schools covered about 14% of the survey area. Fifteen model populations were used, each with the same total number of schools, but different locations, sizes, and densities of school groups.

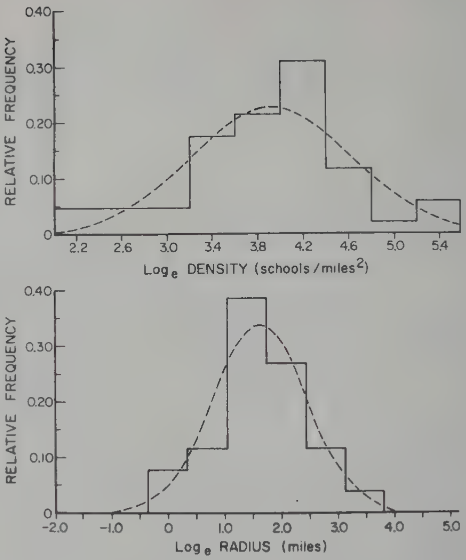

FIGURE 1.—Comparison of distributions of northern anchovy school group density and size observed in the California Current during California Department Fish and Game surveys (solid lines) to log-normal approximations used in simulations (dashed lines).

A simulated survey consisted of a series of transects across the survey area. There were 180 possible transects, each 1 mi wide. Acoustic surveys currently run by the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, used a transect width of 0.14 mi (250 m). Aerial transect widths were typically 0.2 to 0.5 mi. A larger transect width was used in the simulations to hold the model population array down to a reasonable size. We assumed that the general results of the simulations would not change by using a smaller transect width. Since all schools were counted within a transect, the only source of error in the survey estimate was the large variance in the number of schools per transect. For instance, in the model population in Figure 2, the mean number of schools per transect was 835.0, while SD was 920.4 (variance = 8.47×10^5).

Systematic surveys were simulated by counting the schools within a series of transects separated by a constant transect interval. A population estimate was calculated simply by dividing the survey count by the fraction of the survey area covered by the transects. Transect intervals of 2, 3,

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[2] S. J. Crooke. 1975. Cruise reports 75-A-1 and 75-A-6. K. F. Mais. 1976. Cruise reports 76-A-3 and 76-A-9. State of California - The Resources Agency, Department of Fish and Game, Marine Resources Region, Long Beach, CA 90802.

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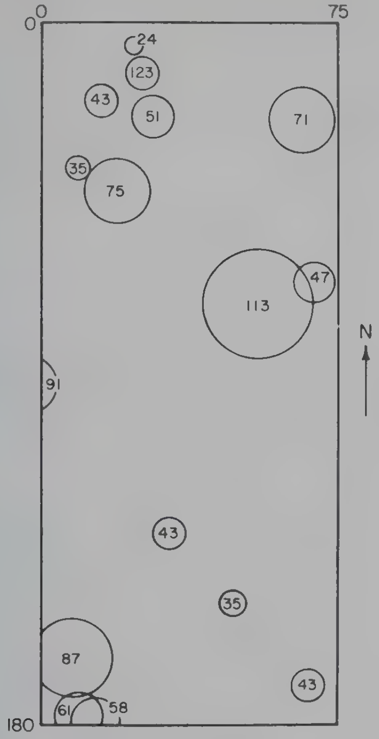

FIGURE 2.—A model northern anchovy population. Densities of school groups in schools per square mile. Simulated survey transects are oriented horizontally. The numbers on the axes are the coordinates of the array and the dimensions, in miles, of the survey area it represents.

4, 5, 7, 10, 12, 15, 20, 25, 30, and 40 mi were used. A survey with a transect interval of *d* miles consisted of 180/*d* transects. For each transect interval, 20 replicate surveys were run by randomly choosing the initial transect from the first *d* transects in the survey area. The replicate survey estimates were used to calculate an unbiased mean population estimate and a coefficient of variation (standard deviation of the replicate estimates divided by the mean), which is a measure of the precision of the estimate (Wiebe 1971). This procedure was repeated on the 15 different model populations.

Random surveys were simluated in an analogous manner to allow a direct comparison of sampling errors. For each of the transect intervals (*d*) of the systematic surveys, 20 replicate surveys were run consisting of 180/*d* transects chosen at random without replacement (a transect was not repeated within a survey). Coefficients of variation were calculated as a measure of precision.

Stratified systematic surveys were simulated after dividing each of the model populations into four 45-mi wide strata. The schools along three transects in each of the four strata were counted to obtain a preliminary estimate of relative population sizes. Then a total of 60, 36, 18, 12, 9, 7, or 6 transects were divided among the strata according to the estimated population fractions. For example, if a stratum contained one-half of the schools counted in the preliminary survey, one-half of the total number of transects was allocated to that stratum for the stratified survey. At least one transect was allocated to each stratum to avoid biasing the final population estimate. For each total number of transects, 20 replicate systematic surveys were run by randomly choosing the initial transect and simulating a systematic survey within each stratum with the allocated number of transects. Once again, coefficients of variation of the replicate population estimates were calculated for each of the 15 model populations.

RESULTS

The results of the systematic survey simulations indicate that the sampling error represented

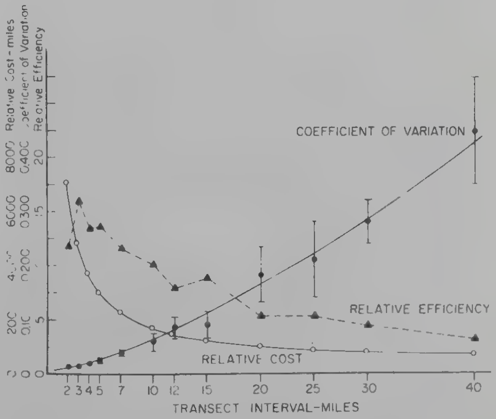

FIGURE 3.—Results of the simulations of systematic surveys of the 15 models for northern anchovy populations. Relative efficiency is proportional to precision (the reciprocal of the coefficient of variation) divided by relative cost (see text). Averages and 95% confidence limits are given for coefficients of variation.

by the coefficient of variation increased as the transect interval increased and sample size decreased (Figure 3). The cost of a survey was assumed to be proportional to the distance covered along the transects plus 360 mi to and from port. Relative efficiency was 10^3 times the reciprocal of the product of the coefficient of variation (C.V.) and relative cost, i.e., precision divided by cost. Efficiency generally decreased as the transect interval increased, but peak efficiency was obtained at a transect interval of 3 mi. By interpolation, it can be seen that a population estimate may range 10 and 25% (2 × C.V.) from the true population size when surveys are run with transect intervals of 8.5 and 16 mi, respectively.

Systematic sampling gave a consistently lower coefficient of variation, or greater precision than random sampling (Figure 4). The variability between model populations, indicated by the confidence limits on the mean coefficient of variation, was greater for the random sampling error ($F_{(14,14)} \geq 5.44$, $P<0.05$ 12) for 8 of the 12 sample sizes. Also represented in Figure 4 are the expected coefficients of variation for random sampling calculated from the model population parameters (σ^2 and μ) by the following equation with a finite population correction:

$$\text{C.V.} = \frac{1}{\mu}\sqrt{\frac{\sigma^2}{n}\left(\frac{N-n}{N}\right)}$$

where σ^2 = the average variance of the number of schools per transect in the 15 model populations = 1,154,636

μ = the mean number of schools per transect = 835.3

n = the number of transects in the survey

N = total number of transects in the survey area = 180.

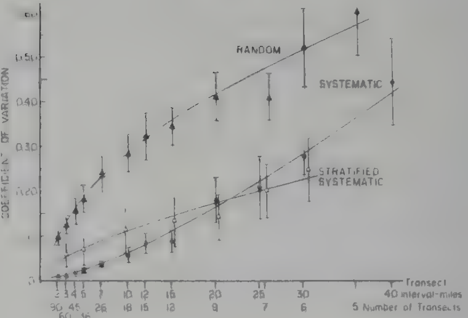

FIGURE 4.—Comparison of the results of the simulations of random, systematic, and stratified systematic surveys. For random surveys, the curve represents the expected coefficients of variation calculated from the parametric variance of the model populations (see text).

For 11 of the 12 sample sizes, the expected value was within 95% confidence limits of the mean observed coefficient of variation. This close agreement supports the validity of the method used to obtain the coefficients of variation in the simulations. There was apparently no significant difference between the coefficients of variation of the systematic and stratified systematic surveys (Figure 4). This was confirmed by analysis of variance (Table 1, $P>0.25$ that there was no added variance due to survey design). However, there were significant interaction effects between survey design and model population ($P<0.01$ that there was no added variance from this source) and between survey design and the number of transects ($P<0.05$).

An attempt was made to elucidate the interactions involving survey design by performing analyses of variance on subsets of the data. It was found that for large sample sizes (transect interval ≤15 mi, or number of transects ≥12) unstratified

TABLE 1.—Analysis of variance of the coefficients of variation from simulated systematic and stratified systematic surveys of model northern anchovy populations. This is a mixed model analysis of variance (Sokal and Rohlf 1969): survey design and number of transects are fixed treatment effects and model population is a random effect.

Source of variation	SS	df	MS	Significance level
Main effects				
Survey design	0.0157	1	0.0157	$F_{(1,14)} = 0.908$, $P>0.25$
Number of transects	1.2872	6	0.2145	$F_{(6,84)} = 56.681$, $P<0.001$
Model population	0.5270	14	0.0376	$F_{(14,84)} = 8.000$, $P<0.001$
Interactions				
Design-number of transects	0.0748	6	0.0125	$F_{(6,84)} = 2.627$, $P<0.05$
Design-population	0.2418	14	0.0173	$F_{(14,84)} = 3.681$, $P<0.001$
Number of transects-population	0.3179	84	0.0038	$F_{(84,84)} = 0.819$, $P>0.50$
Error	0.3988	84	0.0047	
Total	2.8633	209		

systematic surveys were significantly more precise than stratified systematic surveys ($P<0.025$), although there is still a significant interaction between survey design and model population ($P<0.001$). For smaller sample sizes, there was no significant difference between the precision of the two designs.

In the model populations, school groups were located randomly within the survey area. However, the distribution of schools between strata was never random because of the wide range of school group sizes and the small number of school groups in a population. The 15 model populations were divided into three groups (low, intermediate, and high nonrandomness) based on the index of dispersion of the number of schools per stratum. Analysis of variance revealed that for highly nonrandom populations, stratified systematic surveys were significantly more precise than unstratified surveys ($P<0.025$). On the other hand, there was no significant difference between the survey designs for populations of intermediate or low nonrandomness. The effect of the nonrandomness of the populations, in the limited sense used here, is illustrated more dramatically below.

In summary, these results indicate that both the number of transects and the spatial distribution of the population can affect the precision of a survey estimate. The effect of survey design involves complex interactions with the other two factors. These factors should be considered, if possible, when choosing the optimum design for a survey.

DISCUSSION

In general, systematic sampling may result in considerable gains or losses in precision compared with simple random sampling. The greatest increase in precision occurs when there is a high degree of correlation between adjacent sampling units and the correlation decreases as the interval between units increases. In this situation, systematic sampling resembles stratified sampling. On the other hand, precision may be greatly reduced when there is a periodic variation in the population and the sampling interval is equal to this period or a multiple of it (Hansen et al. 1953).

Correlograms between sampling units (transects) in five of the model anchovy populations indicated that transects <10 mi apart had a high positive correlation, while the correlation tended to be slightly negative at distances >20 mi (Figure 5). This autocorrelation structure was due to the frequency distribution of school group sizes. The mean distance at which the autocorrelation function passed through zero was 15.0 mi, while the mean diameter of the individual school groups in the five model populations was 11.8 mi. Distribution of school groups within the model populations was random. However, real populations are likely to be nonrandom in this respect and additional correlations would be expected from this factor. The strong positive correlation between transects separated by short distances explains why systematic surveys with small transect intervals were more precise than random surveys with an equivalent number of transects. As the transect interval increased, the correlation between transects decreased to near zero and the imprecision of systematic sampling approached that of random sampling (Figure 4).

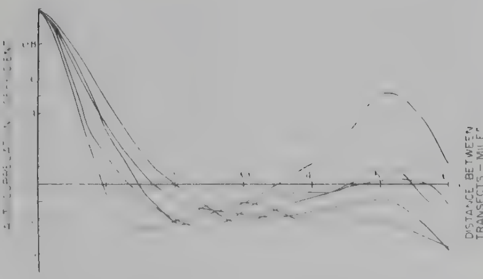

FIGURE 5.—Autocorrelation of transect counts in five model northern anchovy populations.

In order to reduce total sampling error, a common strategy is to allocate effort proportional to the sampling error within parts of a sampling program. The variation observed in the population estimates of the simulated surveys was caused by the large variance in the number of schools per transect. It can be shown in the model populations, as in many biological populations, that the standard deviation was positively correlated with the mean number of schools per transect in a stratum. Therefore, it was thought that the stratified systematic surveys would reduce the total sampling error by allocating more transects where the variance was large. The simulations failed to show any gains in precision from this strategy. This result was not expected, but is possibly due to the random distribution of school groups. The model populations may have been ideal in this sense, but we had relatively little information on the distribution of school groups within the range of the northern anchovy. As stated above, stratified systematic surveys were significantly more precise than unstratified surveys for the five model populations with the most nonrandom distribution of schools between strata. If the school groups themselves are aggregated, it is reasonable to expect an increase in precision by stratifying the survey.

To test this possibility, the simulations were repeated on model populations in which the school groups were limited to only one-half of the survey area. An analysis of variance (Table 2) indicated in this case that the stratified systematic surveys were more precise than the unstratified systematic surveys ($P<0.005$ that there was no added variance due to survey design). The overall mean coefficients of variation were 0.095 and 0.133, respectively. However, there were significant interaction effects involving survey design, indicating that the advantage of stratifying the survey will depend on the number of transects and the spatial distribution of the population. The additional cost of the preliminary survey in the stratified design must also be considered when comparing it with the unstratified design.

The results of the simulated systematic surveys showed that the patchy distribution of schools was an important source of error in estimates of the anchovy population size. Acoustic surveys run by the Southwest Fisheries Center have used transect intervals of 6.6 and 40 mi. The simulations gave evidence that the population estimates from these surveys could be expected to range at least 8 and 90% (2 × C.V.), respectively, from the true population size. The most efficient simulated sampling, in terms of precision per unit cost, occurred at a transect interval of 3 mi. This would require a cruise grid of 4,860 mi, equivalent to a 34-day acoustic survey at 12 kn and 12 h per day, to reduce the coefficient of variation (due to the patchy distribution of schools) to 1.4%. Maximizing efficiency is not a valid goal, however, when the precision gained is greater than that required for the problem of managing the fishery, when other sources of error become more important, and when there are absolute limits on cost. Anchovy population estimates within 25% of the true value might be considered sufficient for management, at least to allow confidence that a consistent change observed over several years is real (pers. commun., P. E. Smith, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif., Oct. 1977).

As stated before, the anchovy population is patchy on two levels: individuals are aggregated into schools and schools are aggregated into school groups. The simulations have quantified the sampling error due to the second level of patchiness only. Although little is known about the distribution of anchovy school groups, it was also demonstrated that their aggregation is potentially an important consideration in designing a survey. The acoustic survey methods currently used by the National Marine Fisheries Service and the California Department of Fish and Game do little more than count the number of anchovy schools (Hewitt et al. 1976; Mais 1974). The Department of Fish and Game calculates a biomass estimate by multiplying the observed school area by a constant factor thought to represent an average biomass per unit area. More sophisticated methods of estimating biomass from the acoustic signal received from a school are now being explored at the Southwest Fisheries Center. For these reasons, the problem of sampling error due to a varying number of fish per school (the first level of patchiness) was not addressed here.

Many sources of error may be involved in an anchovy biomass estimate. Patchiness is important in any type of sampling program. Other sources of error that may be important in an

TABLE 2.—Analysis of variance of the coefficients of variation from simulated systematic and stratified systematic surveys of model northern anchovy populations when the model population school groups are clumped in one-half of the survey area.

Source of variation	SS	df	MS	Significance level
Main effects				
Survey design	0.0732	1	0.0732	$F_{(1,14)} = 12.908$, $P < 0.005$
Number of transects	1.4995	6	0.2499	$F_{(6,84)} = 119.403$, $P < 0.001$
Model population	0.1327	14	0.0095	$F_{(14,84)} = 4.318$, $P < 0.001$
Interactions				
Design-number of transects	0.0476	6	0.0079	$F_{(6,84)} = 3.589$, $P < 0.005$
Design-population	0.0794	14	0.0057	$F_{(14,84)} = 2.591$, $P < 0.01$
Number of transects-population	0.1758	84	0.0021	$F_{(84,84)} = 0.955$, $P > 0.50$
Error	0.1858	84	0.0022	
Total	2.1941	209		

acoustic survey are as follows (Instituto del Mar del Peru 1974; Cram and Hampton 1976; P. E. Smith pers. commun.):

1) Failure to discriminate between anchovy schools and other acoustic targets.
2) Unschooled fish and small schools not detected.
3) Vessel avoidance.
4) Inability to survey in shallow inshore waters.
5) Movement of school groups relative to the survey grid.
6) Fish in the top surface layer missed by the acoustic beam.
7) Errors in the factor for conversion of the acoustic signal information to a biomass estimate.
8) Effect of varying hydrographic conditions on the acoustic signal.
9) Blocking of signal to and from fish far from the ship by fish nearer to the ship.

The magnitude of the error caused by these factors can now only be roughly estimated. They may affect either or both the precision and accuracy of a population estimate. Corrections to reduce the biases are conceivable. The present study has demonstrated the magnitude of the error associated with the patchiness of the anchovy population. Although the model population distributions may be crude approximations to the real distribution, the general conclusions reached here are not likely to be changed by adding further levels of complexity to the model. The sampling error due to patchiness can be reduced by properly designing a survey, but never eliminated. Temporal and spatial differences in population estimates must be interpreted with an awareness that the error exists.

ACKNOWLEDGMENTS

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7814

SEA SENSE

TUNA/DOLPHIN PROGRAM

Five Years of Progress

by William W. Fox, Jr.

The United States Congress passed the Marine Mammal Protection Act (MMPA) on October 21, 1972. Among other things, the Act addresses the problem of dolphin mortality which occurs incidentally in a significant portion of purse seine fishing for yellowfin tuna in the eastern Pacific Ocean. The MMPA established a twenty-four-month period that gave the tuna fishery a temporary exemption from the moratorium provisions of the Act, provided that all known gear and procedures which minimized harm to marine mammals, were used. The two-year period also gave the National Marine Fisheries Service (NMFS) time to develop new gear and procedures for reducing dolphin mortality and to obtain the requisite information for bringing the tuna fishery under the permit provisions of the Act.

Following passage of the MMPA, the already-existing NMFS dolphin research program at the La Jolla, California, Laboratory of the Southwest Fisheries Center was greatly expanded to develop gear and procedures for reducing the incidental dolphin mortality and to determine the status of the sub-populations of the impacted dolphin stocks. The expanded research program was fully operational by mid-1973. However, barely a year later, the scientists of the research program had to prepare a report on their progress. The report was required for legal hearings to bring the tuna fishery under the permit provisions of the Act by October 1974, the expiration date of the twenty-four-month exemption. After public hearings before an Administrative Law Judge (ALJ), NMFS issued a general permit to the tuna fishery for the 1975 fishing season and modified the regulations covering the tuna fishery to include several new procedures developed through the research program and recommended by the ALJ. Several environmental organizations immediately filed suit to void the general permit.

While the lawsuit over the 1975 permit was pending, NMFS held hearings in late 1975 on modifications in the marine mammal regulations governing the tuna fishery for the 1976 fishing season. NMFS issued a general permit for the 1976 fishing season and again several environmental organizations filed suit to void the new permit.

The two lawsuits were consolidated and heard by Judge Charles Richey of the United States District Court. On May 11, 1976, Judge Richey decided in favor of the environmental groups. He voided the permit issued to the tuna industry by NMFS because (1) it was his opinion that certain statements about the dolphin populations which were not published in issuing the permit are so required by the MMPA and (2) the permit did not specify the exact number and kind of animals that may be taken. On very important points of policy, Judge Richey further ruled that the primary consideration shall be that the taking, allowed by the permit, shall not be to the disadvantage of the dolphin populations and that the burden of proof lies with the applicant, in this case the tuna industry.

Obscured behind all this highly visible legal wrangling was the success of the research program in developing gear and procedures to reduce the incidental dolphin mortality and in determining the impact of the incidental mortality on the dolphin stocks. Also obscured was the steady progress that the United States tuna purse seine fleet achieved in reducing the dolphin mortality rate.

Last November Oceans *published an article on the incidental porpoise mortality during seine fishing for yellowfin tuna. Here is another perspective by Dr. William W. Fox, Jr., Chief Scientist responsible for the National Marine Fisheries Service's tuna-porpoise research program.*

Progress in Dolphin Mortality Rate Reduction

Until the middle of 1976, when a quota on the number of dolphins that could be killed incidental to tuna fishing was instituted as a result of Judge Richey's ruling, the gear and procedures defined in the NMFS regulations dealt with the mortality rate, i.e., the number of animals killed during a given set of the purse seine. In any given set, the number of dolphins killed is influenced by the number and kind of dolphins in the net and the amount of yellowfin tuna caught; these conditions differ widely among fishing seasons. Comparison of the mortality rates of sets under similar conditions reveals that there were substantial and continuous reductions in the mortality rate of 28%, 22%, 18%, and 65%, each year from 1973 through 1977, respectively.

The total dolphin mortality that occurs in a given year depends on the amount of fishing done in association with dolphins, as well as the dolphin mortality rate. The annual catch of yellowfin tuna associated with dolphins after passage of the MMPA (1973-1977) has averaged about 114,000 tons, the highest being 127,000 tons in 1973 and the lowest being 99,000 tons in 1974. The annual mortality of marine mammals incidental to United States tuna purse seine fishing for 1971 and 1972, the two years immediately prior to passage of the MMPA, averaged 309,000 animals. Our estimates indicate that the annual mortality was even higher during several of the previous years. During 1973 and 1974, the twenty-four-month exemption period provided by the MMPA, the yellowfin catch associated with dolphins averaged 113,000 tons and the dolphin mortality averaged 137,000 animals per year under NMFS regulations and industry-wide adoption of all known gear and procedures which minimized harm to the dolphins. Therefore, over 340,000 dolphins were saved during the two-year period, despite an increase in the catch of yellowfin tuna associated with dolphins, from 106,000 tons per year in 1971 and 1972 to 113,000 tons per year in 1973 and 1974. Further progress was made in 1975 through 1977 as the annual mortality of dolphins was reduced to 134,000, 104,000, and 27,000 animals, respectively, while the yellowfin tuna catch associated with dolphins increased slightly to an average of about 115,000 tons per year, 1975-1977.

By the end of 1977 the dolphin mortality rate and the annual dolphin mortality had decreased to less than 10% of the level that existed prior to enactment of the MMPA. This was due to the gear and procedures developed by the NMFS research program and the tuna industry, embodied in NMFS regulations, and applied with increasing diligence over the years by the fishermen of the United States tuna purse seine fleet.

The major breakthrough in 1977 had its roots in late 1975, barely two years after the expanded research program began, when an NMFS charter cruise of the M/V *Bold Contender* demonstrated the capability of the total NMFS system of gear and techniques to reduce greatly dolphin mortality. The *Bold Contender* made 25 sets with a mortality rate of only 1.44 animals per set (15 of the sets killed no animals) as compared with 12.80 animals killed per set for the comparable fleet average in 1975. Because of the remarkable success of the *Bold Contender* charter, a massive test of two modifications of this system was planned for early 1976. The purpose of this test, involving twenty purse seiners, was to determine whether or not the very low mortality rate achieved by the system on the *Bold Contender* charter was feasible under competitive fishing conditions and feasible for most tuna purse seine vessels. The experiment was a joint project of NMFS, the Marine Mammal Commission, and the tuna industry-sponsored Porpoise Rescue Foundation.

Unfortunately, the very ruling by Judge Richey on May 11, 1976, sought and won by the environmental groups, greatly interrupted the 1976 twenty-vessel test. The effects of the ruling prevented the data from being collected completely until the end of 1976 and imposed conditions that made analysis and interpretation of the results very difficult. Several problems with the system were noted during the 1976 twenty-vessel test, and a charter cruise of the M/V *Elizabeth C. J.* from October through December of 1976 successfully tested modifications designed to alleviate those problems. However, final analysis of the data could not be completed until late spring of 1977, too late for full incorporation in the 1977 regulations.

The obviously beneficial gear and procedures from the 1976 twenty-vessel test and the *Elizabeth C. J.* charter cruise; primarily the extensive use of fine mesh webbing in the net to reduce entanglement and a man with a face mask in a raft inside the net to determine if all live animals have been rescued before the net and fish are hauled aboard; were incorporated in the 1977 regulations. These gear and procedures contributed substantially to the phenomenally reduced dolphin mortality rate per set and the total mortality for 1977. Entanglement of animals in the net dropped from an average of six to seven animals per set in 1976 to less than one per set in 1977 for sets where animals were killed; the average number of animals killed when the net and fish were hauled aboard dropped from one per set in 1976 to less than one in ten sets in 1977 for sets where animals were killed; and the percentage of sets with no animals being killed rose from forty percent in 1976 to sixty percent in 1977. While the United States tuna fleet remained in port for nearly three months during 1977, preliminary data indicate that the amount of yellowfin catch associated with dolphins in 1977 was near the average amount for the previous four years. Therefore, the low mortality of 27,000 dolphins in 1977 was due almost exclusively to the mandated gear and procedures, and to the diligent efforts of the United States tuna fishermen.

The modified gear tested by the M/V *Elizabeth C. J.* was fleet-tested on nineteen vessel trips during the 1977 season from late May through December; again, this test had been extensively delayed because of the complications raised by Judge Richey's ruling. Vessels testing this gear had a dolphin mortality rate during 1977 of about half that of the other vessels in the fleet; this gear is required under NMFS regulations for 1978. Obscured by all the legal battles is the ironic fact that, in effect, the suit brought by the environmental groups and decided by Judge Richey delayed implementation of the most effective dolphin rescue gear by about one year.

Progress in reducing the dolphin mortality rate is continuing in 1978. The dolphin mortality rate during the first quarter of 1978 has been about twenty percent below the 1977 level. The vessels using the newly required gear, termed the porpoise apron, currently have a dolphin mortality rate of about sixty percent below that of other vessels, which must install the new gear by July 1, 1978.

NMFS scientists had formed estimates of existing dolphin population sizes and had determined the impact of fishing-caused mortality levels on existing population sizes for the two major (i.e., accounting for over eighty percent of the incidental mortality) dolphin stocks as background for the hearings held in 1974 and 1975 on the issuance of the permits disputed by the environmental groups. This information, however, was not published in the form that Judge Richey ruled is required by the MMPA, nor did it cover each of the twenty-one dolphin species or stocks involved in the tuna fishery. The primary stumbling block in performing the population assessments in the manner prescribed by Judge Richey, aside from the personnel limitations of our research program, was the lack of an intelligible or a generally accepted scientific definition of the term "optimum sustainable population" contained in the MMPA.

After the scientists in my research program conducted an accelerated project of assembling all relevant data and population parameter estimates, in July, 1976, I convened a workshop of twelve international scientists, most of whom are recognized experts in the field of population assessment. They agreed upon a working definition of optimum sustainable population, since adopted formally by NMFS, and developed assessments of all twenty-one dolphin species or stocks in the manner dictated by Judge Richey's ruling. The results of the workshop, which confirmed our previous assessment of the major dolphin stocks, were published in a report made available to the public in September 1976.

The 1977 permit and regulations issued by NMFS were based on the workshop's report. The population assessments involve a certain degree of imprecision as well as several major assumptions; therefore, the quotas established for 1977 were very conservative. While the aggregate estimate of the amount of United States-caused dolphin mortality that would allow the stocks to remain stable was 179,000 animals, the sum total of quotas set by NMFS for most species and stocks was only 62,429 animals. Furthermore, the eastern spinner dolphin stock, historically a major fished stock, was declared to be depleted by NMFS, and no intentional taking was allowed. Subsequent to the issuance of the 1977 regulations, the Committee for Humane Legislation, Inc., filed another suit to void them; the suit was also heard by Judge Richey. However, this time on June 30, 1977, he ruled in favor of

NMFS and commended us for our population assessment work.

For the first six months of 1977, we conducted a major survey of the cetacean (dolphin and whale) populations of the eastern tropical Pacific Ocean. We used two aircraft and two research vessels to cover the approximately four million square-mile area. The data collected are currently under analysis, and the results will be used to improve our assessment of the status of the populations.

Substantial progress has been made in reducing the dolphin mortality incidental to United States tuna purse seine fishing and in determining the status of the affected dolphin populations. However, considerably more research is required before we can become complacent about the status of the dolphin populations or before we can virtually eliminate dolphin mortality incidental to tuna purse seine fishing.

Our research at the Southwest Fisheries Center is continuing to refine our knowledge about the dolphin population parameters through intensive at-sea sampling and a major dolphin mark-recapture experiment. Another major survey of the cetacean populations in the eastern Pacific Ocean is planned for early 1979, and intensive localized surveys are planned for subsequent years. Now that the direct observable mortality has been reduced to such a low level, we have expanded our investigation of the effects of the pursuit and capture process on the dolphin populations. We are also examining more closely the ecological relationship between yellowfin tuna and the dolphins, since the primary objective of the MMPA is to "maintain the health and stability of the marine ecosystem."

Our research into improved fishing techniques, which will further reduce the incidental dolphin mortality, has expanded in funding and direction this year. We have begun a project dealing specifically with the behavior of dolphins and tuna; we have cooperated in and supported the funding for research on acoustics and artificial aggregating devices by the National Science Foundation; and we have funded contracts investigating the sensory systems of tuna—all leading to improved tuna fishing systems which may eventually allow capture of tuna associated with dolphins without also capturing the dolphins. Only through the development of such fishing systems, which are economically more efficient than simultaneously capturing the entire tuna and dolphin aggregations, can incidental dolphin mortality be virtually eliminated. ■

TROPHIC RELATIONSHIPS AMONG FISHES AND PLANKTON IN THE LAGOON AT ENEWETAK ATOLL, MARSHALL ISLANDS

EDMUND S. HOBSON AND JAMES R. CHESS[1]

ABSTRACT

Trophic relationships among fishes and zooplankters in the nearshore lagoon at Enewetak differ sharply between day and night, and are strongly influenced by current patterns. Adults of most diurnal planktivorous fishes are numerous in certain places where tidal currents are strong, but few where such currents are consistently weak. Thus, the sea bass, *Mirolabrichthys pascalus;* the snapper *Pterocaesio tile;* and the damselfishes (*Chromis agilis, C. caerulea, C. lepidolepis, C. margaritifer,* and *Pomacentrus coelestus*) are numerous in strong-current areas near interisland passes, but relatively few or absent in weak-current areas close in the lee of islands or interisland reefs. The former areas are rich, the latter poor, in the major prey of these fishes—copepods, larvaceans, and fish eggs. On the other hand, the zooplankton-poor waters close in the lee of islands and interisland reefs are rich in debris from the reefs, and fishes that can subsist on these materials are abundant. *Dascyllus reticulatus* is numerous here, although less so than where currents are strong, and takes algal fragments as an important, if secondary, part of its diet; *Pomacentrus vaiuli,* equally abundant in both strong- and weak-current areas, feeds largely on algal fragments, as does *P. pavo,* which is more numerous here than where currents are strong.

In contrast, the major nocturnal planktivores are concentrated where currents are weak, but relatively sparse where these currents are strong. Included are: the soldier fishes *Myripristis pralinus* and *M. violaceus,* and the cardinalfishes *Apogon gracilis* (young also feed by day), *A. novaeguinae,* and *A. savayensis.* They are strictly carnivores that prey mostly on larger zooplankters—including large calanoids, mysids, isopods, gammarids, postlarval carideans, and brachyuran megalops—absent (except for the mysids) in the nearshore water column by day. These prey organisms generally find conditions unfavorable where strong currents flow. Most of them are sheltered on or near specific nearshore substrata during the day and enter the water column only at night; but others are in deeper water offshore by day and move inshore at night after rising toward the surface.

Limited evidence indicates that planktivorous juvenile and larval fishes, as well as the tiny plankters on which they feed, follow patterns different from those followed by larger individuals.

Many nearshore fishes find most of their food among the plankton. Clearly, the water column is a rich feeding ground. Nevertheless, fishes that would take plankters face problems perhaps not immediately apparent. Consider, for example, the feeding-related morphologies of planktivorous fishes, which obviously are products of strong selection pressures. Fishes that take plankters by day are characterized by modifications of head and jaws, including dentition, that permit even relatively large individuals to effectively consume tiny organisms in midwater, whereas fishes that take plankters at night tend to be large-mouthed species with specialized means to detect, and capture, the larger organisms that are in the nearshore water column only after dark. Awareness of these facts evolved from studies in tropical seas (Hobson 1965, 1968, 1972, 1974; Starck and Davis 1966; Davis and Birdsong 1973) and was emphasized in more detailed study in warm temperate waters of southern California (Hobson and Chess 1976). Additional study has shown that many fishes which take plankters by day accentuate fusiform bodies and deeply incised caudal fins—features that promote rapid swimming, and which, significantly, are undeveloped among their nocturnal counterparts. Increased speed, it was suggested (Hobson 1974, 1975; Hobson and Chess 1976), has given diurnal planktivores that swim in the water column quicker access to shelter in response to severe pressures from piscivorous predators; that these speed-inducing features are comparatively undeveloped among the nocturnal species, the suggestion continued, reflects a sharply reduced threat from piscivorous predators in the water column after dark.

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[1] Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

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The present paper considers these aspects of the interactions among the plankton and adult planktivorous fishes as expressed in the lagoon of a coral atoll. It is based on a study over 21 days at Enewetak, Marshall Islands, during April 1976.

STUDY AREA

Enewetak Atoll (lat. 11°26′N, long. 162°22′E) is a ring of shallow coral reefs and low islands encircling a lagoon about 37 km north to south and 56 km east to west. It sits amid the westward flowing North Equatorial Current and was buffeted throughout our visit (as during most of the year) by trade winds from the east. So with surface waters generally moving to the west, it was not surprising that tidal currents in passes between the open ocean and the lagoon on the windward side of the atoll were strong on the flood, but weak on the ebb. Furthermore, water over the windward interisland reefs, driven by the incessant trade winds and seas breaking over the outer reef, flowed in just one direction—into the lagoon. Presumably the situation was reversed on the leeward side of the atoll, as described for Bikini and Rongelap, two other Marshallese atolls (von Arx 1948).

From most islands, and interisland reefs, a narrow shelf of sand and isolated patch reefs extend several hundred meters into the lagoon. At the outer edge of this shelf, where the water in most places is about 20 m deep, the sea floor drops sharply to about 50 m, which is the approximate water depth over much of the lagoon. Our study centered on the lagoon's nearshore shelf along the eastern (windward) side of the atoll, where the waters are sheltered from the trade winds and prevailing seas. Initially, we made observations from Aoman Island in the north, to Enewetak Island in the south—a distance of about 32 km. Underwater visibility ranged from about 5 to over 30 m, and so at all times was suitable for observing activity. From these observations we gained a general impression of how the planktivorous fishes were distributed, as well as something of their activities.

It was soon apparent that the distribution of the planktivorous fishes was strongly influenced by nearshore current patterns. This knowledge permitted us to select fruitful locations for more intensive work, including sampling the plankton and gut contents of planktivorous fishes. Because time was short, we limited intensive study to two sites that represented opposing extremes in prevailing current velocities, weak and strong—a variance that proved to identify certain major influences on fish-plankton interactions.

Currents were weak or nonexistent at our site in 7 m of water among coral heads on level sand about 100 m from Walt Island, close in the lee of the interisland reef (Figure 1, site A). These weak currents were most evident when water covered the reef, and always flowed from the reef. We made observations here at all hours of day and night during both spring and neap tides, and our collections sampled the full range of currents encountered, from no perceptible water movement to a velocity of 9 cm/s.

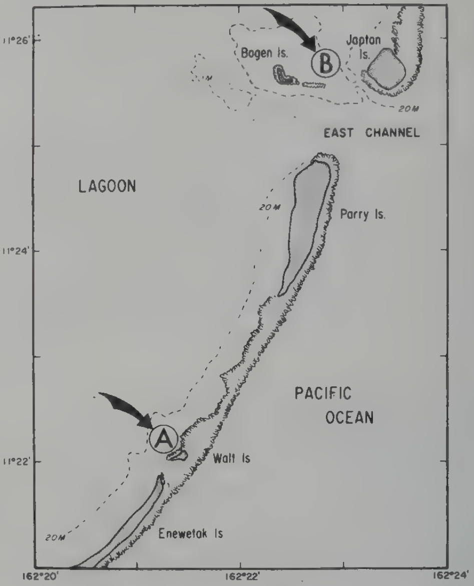

FIGURE 1.—The study area, Enewetak Atoll, Marshall Islands.

Strong tidal currents fed by water entering the lagoon through East Channel periodically swept through our site in 13 m of water among coral heads on gently sloping sand about 600 m windward of Bogen Island (Figure 1, site B). During our sampling here, currents ranged from 15 to 90, $\overline{x} = 51$, cm/s, always on flood tide. Observations (but no sampling) were also made at this station at slack water and during ebb tide when there was little perceptible current. Although there was scant evidence of an ebb current at the collection site, a slow outflow from the lagoon was evident in East Channel itself. Even though strong currents at this site were limited essentially to flooding spring tides, their impact was clearly visible on the substrate at all times. Most notable, the sand, which swirled about in the stronger currents, was piled high in the lee of the patch reefs.

METHODS

Plankton

The methods used to collect plankton differed between the two primary sites owing to the contrast in prevailing current velocities. Nevertheless, all collections employed the same 0.333-mm mesh net and produced comparable assessments of the plankton at the two places, particularly between day and night.

Collecting Where Currents Were Weak

When sampling at the Walt Island site, we pushed the net through the water around one patch reef (Figure 2), a circuit that always took 5 min. The procedure was similar to that used at Santa Catalina Island, Calif. (Hobson and Chess 1976). When swimming with the net by day, we could watch organisms in its path, and this gave us insight into which of them might be evading the net. Mysids, for example, could do so, and often did. But these organisms reacted to us less than expected, perhaps because the meter net's opening was large, and its approach was slow and quiet. Certainly our collections would have sampled these large mobile forms less effectively if the net had been preceded by the harness and tow line used when operating from a boat.

Three series of collections were made during midday (between 1000 and 1400 h), and three series were made at night (1 h after last evening light, at midnight, and 1 h before first morning light). We spaced the noctunal collections over the night because earlier work had suggested that certain organisms are in the water column only briefly during specific periods of the night, a phenomenon we did not find among the diurnal plankters (Hobson and Chess 1976). Of the three collections in each series, one was made within 1 m of the bottom, one midway between bottom and surface, and one with the net breaking the surface. At night, ambient light in this clear water over white sand permitted us to collect without diving lights. Our stay at Enewetak spanned the period from full to new moon, so that we sampled both spring and neap tides, but generally there was no moonlight during the collections owing to cloud cover or time of night.

Net speed was 28 cm/s, as calculated from readings of a current meter calibrated by the speed at which the smallest fragments of algae visible to us drifted along a measured course. We decided it was necessary to determine net speed only once at this station, because all collections were made by the same two swimmers who each time exerted about the same effort, and covered the same distance.

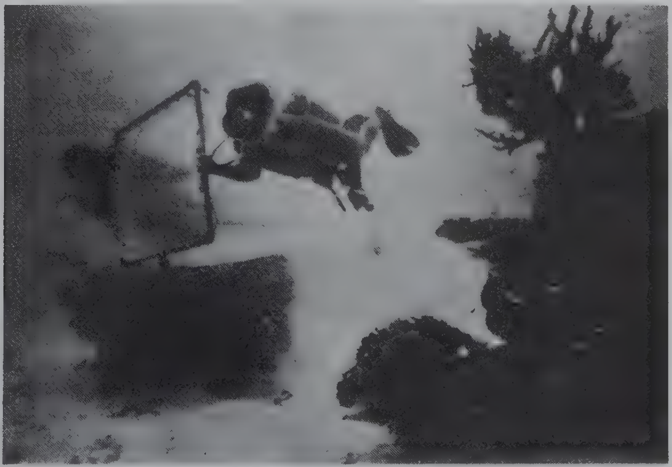

FIGURE 2.—Collecting plankton at Walt Island, Enewetak Atoll, site of weak currents. The square frame permitted more accurate assessments at the surface and close to the sea floor.

Collecting Where Currents Were Strong

All collections at Bogen Island were made at the height of flood tide, when currents often were too strong to swim with the net, so here we worked from a boat anchored fore and aft above the study site. The net was secured to a line that passed from the boat, through a block anchored on the reef below, and returned to the boat. It was positioned at the three collecting depths—bottom, middepths, and surface—by pulling the line one way or the other through the block (Figure 3). The collections were extended to 15 min (compared with 5 min at the other station) to reduce error introduced by organisms taken during the few seconds it took to raise and lower the net. In presenting these data, however, we make the values equivalent to a 5-min collection. These collections depended on the current (which was measured with every collection) to carry plankton into the net, and the weakest current sampled, 15 cm/s, was judged close to the minimum necessary. Two series of collections were made during the day—at midday and in midafternoon—and two series were made at night—1 h after last evening light and at midnight.

There are problems in comparing data collected by these different methods at the two stations, but we had the advantage of sampling precisely defined positions—a critical requirement when relating the plankton to food habits of specific fishes.

The volume of water filtered by this stationary net varied with the different current velocities, which strongly influenced the numbers of plankters taken. Nevertheless, these numbers accurately reflect the relative numbers of plankters available to fishes feeding in these currents. On the other hand, differences in volumes of water sampled must be considered when comparing estimates of the plankton in the water column from one time or place to another. Therefore, plankton volumes from the strong-current site are presented two ways: volumes actually sampled and volumes adjusted for current differences. In adjusting for current, the volumes in all collections were made equivalent to those taken in a net moving at the same relative speed that we pushed the net at the Walt Island site—28 cm/s. These adjustments also permit rough comparisons with data from California (Hobson and Chess 1976), where plankton were collected in the same way and by the same swimmers.

Fishes

A total of 154 fish specimens of 16 species were speared immediately after the plankton collections. Species names are those used by Schultz et al. (1953, 1960), except where more recent taxonomic study has indicated change.

The specimens were preserved in 10% Formalin[2] immediately after collection. Later, food items in the gut were identified and their positions in the gut noted. The following data were recorded for

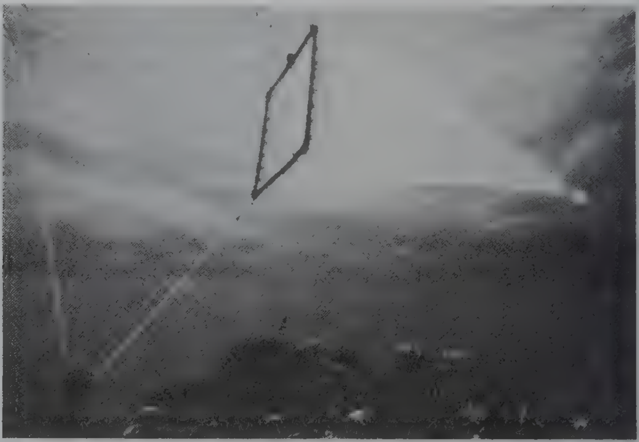

FIGURE 3.—Collecting plankton at Bogen Island, Enewetak Atoll, site of strong currents.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

items of each food type: 1) number, 2) size range, 3) state of digestion (subjectively assessed on a scale of 5, from fresh to well-digested), and 4) an estimate of their representation among the gut contents as percent of the total volume.

RESULTS

Our widespread observations along the sandy shelf which rims the lagoon established that the planktivorous fishes were centered about the isolated patch reefs. At least a few planktivores foraged in the water column above virtually every reef, but more of them were above some reefs than others and there were clear patterns to their distributions. For example, during the day there tended to be more planktivores above reefs at the outer edge of the shelf than above similar reefs at comparable depths, and shallower, shoreward on the shelf. But diurnal planktivores were most numerous where strong tidal currents flowed through passes from the open sea, and least numerous where reefs or islands blocked the flow of water into the lagoon. On the other hand, the reverse was true of the nocturnal planktivores. Because the distributions and activities of these fishes proved to be closely related to current patterns, we judged that the contributing influences are best isolated by concentrating on the more extreme current situations. This was true even though in most places over the range of our observations currents were variably moderate, and prevailing conditions intermediate between the two extremes.

Where Currents Were Weak

General Observations

There is relatively little water movement near the lee shores of the islands and close behind the interisland reefs that block entry of water into the lagoon from the open sea. In some of these locations there is enough circulation to permit rich coral growth and underwater visibility that exceeds 15 m, but in other places the circulation is more limited, and living corals exist as small heads or encrustations on otherwise dead reefs, while underwater visibility often is <5 m. The lagoon floor in these regions generally is of relatively undisturbed, fine-grained sand. (A sample of sediment from the Walt Island site proved to be 75% foraminiferans, with a density of 1.32 g/ml. Grain size in over 80% of this sample was <1 mm.)

PLANKTON.—Usually we made no effort to detect the smaller plankters during our general diurnal observations, even though many of the copepods and others were visible with close inspection. Dense swarms of mysids, however, were outstanding features of the daytime scene in many places where currents were weak, especially above sand close to the patch reefs. With increasing distance from the bottom, their swarms were smaller and less numerous, though swarm-members always were closely spaced. Juveniles predominated at the lower levels, adults were more numerous above. The swarms dispersed at night, when both adults and juveniles scattered near the bottom and at middepth, but only adults were near the surface.

Although mysids were the only plankters routinely noted during the day, others were prominent after dark. Most conspicuous were large calanoid copepods—larger than any copepods present in daylight—that for a few hours after last evening light swarmed around us in dense numbers whenever we turned on our diving lights. Highly motile epitokous nereids, as well as an opheliid, *Polyophthalmus* sp., were numerous polychaetes, with other forms including hyperid and gammarid amphipods, stomatopod larvae, reptantian zoea, and brachyuran megalops. None of these forms were seen in daylight.

FISHES.—Adult diurnal planktivorous fishes were relatively few in these surroundings compared with their numbers elsewhere. Nevertheless, this seemed a favored habitat for at least one species, *Pomacentrus pavo,* which was widespread in groups of four to six individuals 2 to 5 cm above low coral-rock outcroppings in the sand, usually in the vicinity of patch reefs. *Pomacentrus vaiuli,* another abundant species, was present only as solitary individuals that rarely moved more than a few centimeters from the larger patch reefs, yet most of its food was small organisms swimming or drifting free in the water immediately adjacent to the substrate. *Dascyllus reticulatus* was numerous by day in feeding aggregations up into the midwaters, usually above large heads of branching corals, while at the same time *Amblyglyphidodon curacao,* which usually fed in groups of <10, often ranged up to the water's surface. Of the diurnal planktivores considered here that ranged into the water column, *D. reticulatus* and *A. curacao* were the only deep-bodied forms. Other diurnal planktivores were more sparse. The more prominent of these were species of *Chromis* that usually stayed within 2 m of the reef. *Chromis caerulea,*[3] mostly juveniles, generally hovered in small aggregations above heads of the coral *Pocillopora,* but *C. agilis* and *C. margaritifer* more often were solitary or in groups of just a few. At night all of these fishes were under reef shelter, and we saw no evidence of them feeding at that time.

Despite the relative paucity of adult diurnal planktivores in this habitat, planktivorous juveniles and larvae of at least several fish species frequently were numerous and fed by day. An outstanding example was the juveniles of *Apogon gracilis,* well under 50 mm long, which hovered in large, umbrella-shaped aggregations above coral heads in open sand (Figure 4). Dense schools of larval fishes, 7 to 10 mm long, (often taken on first glance as mysid swarms) were sometimes prominent, but so close to the reefs that our net sampled only an occasional outlier.

Although adult diurnal planktivores were comparatively sparse in this habitat, their nocturnal counterparts tended to be especially numerous. During daylight, dense, inactive concentrations of *Myripristis* spp. abounded at openings of reef crevices. Prominent as these concentrations were, they represented only a small part of the tremendous numbers of their species packed into the reef interstices. We became fully aware of the immensity of these populations when, about 30 min after sunset, they abruptly streamed into the open and entered the water column. Shortly after emerging, most individuals of one species, *M. murdjan,* apparently moved elsewhere, because though they were numerous initially, relatively few were seen during the night, and their numbers did not in-

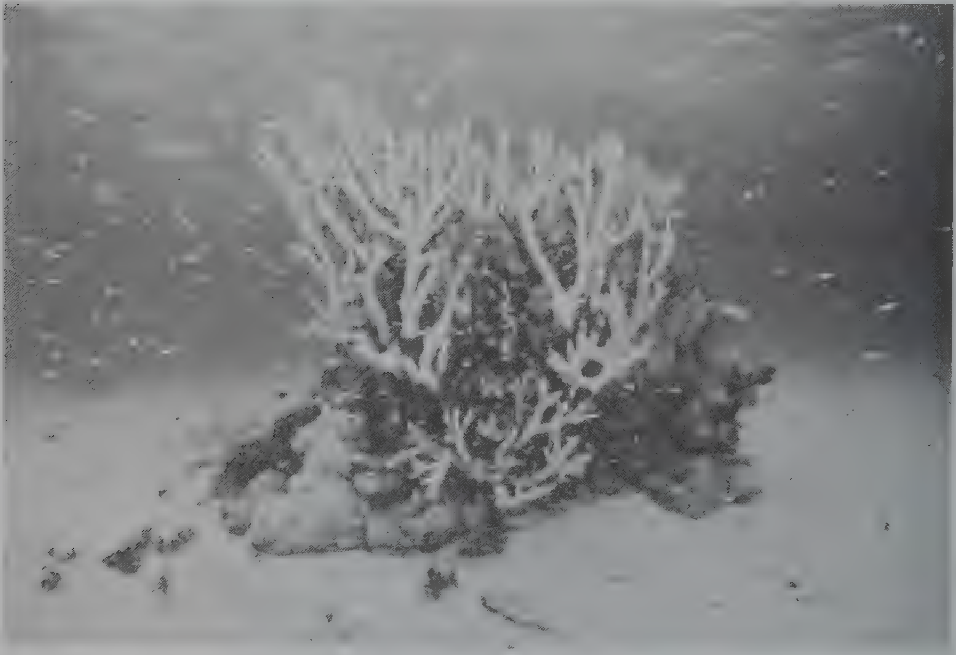

FIGURE 4.—Juvenile cardinal fish, *Apogon gracilis,* approximately 25 to 30 mm long, feeding on plankton by day where currents are weak.

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[3] At the distances that most of our observations were made, we were unable to consistently distinguish *Chromis caerulea* from the very similar *C. atripectoralis,* and so referred all observations to the former. Significantly, however, the behavior attributed to this species is consistent with that in all individuals observed.

crease again until just before dawn. In contrast, large numbers of *M. pralinus* and *M. violaceus* remained concentrated in the waters above the nearshore patch reefs throughout the night.

Also prominent in daylight were *Apogon* spp., which concentrated close to reef cover. These included adults of *A. gracilis,* which schooled quietly at the bases of the same coral heads above which juveniles of the species (see above) actively fed; nevertheless, the true numbers of apogonids were fully appreciated only after nightfall, when many large species unseen during the day emerged from reef shelters. The most prominent of the larger apogonids entering the water column was *A. savayensis,* although some of the smaller species, notably *A. gracilis* and *A. novaeguinae,* were more numerous. Larger apogonids were solitary at night, but smaller ones often were loosely aggregated, including *A. gracilis,* of which the adults joined the juveniles in the water column after dark.

TABLE 1.—Composition of plankton at Walt Island, Enewetak Atoll, site of weak currents.

	Day (*n* = 9)		Night (*n* = 9)	
Materials	Mean vol (ml)	Mean % of total vol	Mean vol (ml)	Mean % of total vol
Zooplankters	3.4	38.3	10.7	79.0
Algae fragments	3.6	51.8	3.1	21.0
Crustacean molts	0.5	9.9	0.0	0.0
Totals	7.7	100.0	13.8	100.0

Samples From Walt Island

PLANKTON.—Major materials (zooplankters, algae fragements, and crustacean molts) taken in the plankton net during day and night at the Walt Island site of weak currents are listed in Table 1. Zooplankters, grouped by major taxonomic categories and with data pooled from the three sampled depths (surface, middepth, and near bottom), are listed in Table 2. Additional data for calanoid copepods are presented in Table 3 to support certain points developed in the Discussion.

TABLE 3.—Size distribution of calanoid copepods, day and night, at Walt Island, Enewetak Atoll, site of weak currents.

	Midday		Night			
	(*n* = 9)		1 h after last light (*n* = 3)		Midnight and later (*n* = 6)	
Size (mm)	Percent	Mean no.	Percent	Mean no.	Percent	Mean no.
>3-5	0	0	0	0	24	[1]138.7
>2-3	0	0	0	0	31	[2]180.5
>1-2	48	[3]10.9	43	[4]40.1	31	[5]179.0
<1	52	11.8	57	53.2	14	81.3

[1] Including *Euchaeta marina, Pleurommama xiphias,* and *Undinula vulgaris.*
[2] Including *Candacia* sp., *E. marina, Neocalanus* sp., *Pleurommama xiphias,* and *U. vulgaris.*
[3] Including *Acartia* sp., *Metridia* sp., *Pleurommama* sp., and *Scolothricella* sp
[4] Including *Acartia* sp., *Candacia* sp., *E. marina,* and *U. vulgaris*
[5] Including *Acartia* sp., *Candacia* sp., and *Euchaeta* sp.

TABLE 2.—Occurrence, number, and size of zooplankters collected day and night at Walt Island, Enewetak Atoll, site of weak currents.

	Day (*n* = 9)			Night (*n* = 9)		
Plankton categories present	Size (mm)	Percent occurrence	Mean number	Size (mm)	Percent occurrence	Mean number
Foraminiferans[1]	0.4-1.0	100	36.7	0.4-2.0	100	337.0
Siphonophores	4.0-6.0	11	0.4	4.0-8.0	38	2.6
Polychaetes	—	0	0.0	3.0-25.0	33	28.3
Mollusk larvae	0.3-1.0	78	21.0	0.5-2.0	89	55.2
Pteropods	—	0	0.0	2.0-5.0	33	2.0
Squid	—	0	0.0	3.0-12.0	22	0.3
Ostracods	0.5-1.0	67	5.4	0.6-2.0	100	26.4
Calanoid copepods	0.5-2.0	89	22.7	0.5-5.0	100	579.5
Cyclopoid copepods	0.5-1.5	56	8.0	0.5-2.0	100	39.0
Harpacticoid copepods	0.5-1.0	22	0.3	0.5-2.0	89	9.3
Stomatopod larvae	—	0	0.0	18.0-26.0	11	1.0
Mysids	2.0-8.0	89	[2]1,398.7	1.0-8.0	100	[3]3,031.8
Cumaceans	—	0	0.0	1.0-1.5	56	12.4
Isopods	—	—	0.0	1.0-12.0	67	5.3
Hyperiid amphipods	0.6-2.0	33	5.0	1.0-4.0	100	17.8
Gammarid amphipods	—	0	0.0	1.0-5.0	100	23.2
Caridean larvae	2.0-3.0	89	6.0	1.0-12.0	100	504.2
Caridean adults and juveniles	—	0	0.0	4.0-15.0	100	20.0
Reptantian zoea	0.5-2.0	78	20.0	0.5-4.0	100	629.8
Brachyuran megalops	2.0-3.0	22	0.2	2.0-8.0	100	60.3
Chaetognaths	4.0-10.0	44	1.0	3.0-12.0	100	92.4
Larvaceans	—	0	0.0	2.0	11	0.4
Apendicularian larvae	2.0	11	0.1	2.0	11	0.4
Fish eggs	1.0-2.0	100	40.0	0.5-3.0	100	273.6
Fish larvae	2.0-13.0	44	11.3	2.0-25.0	100	51.2

[1] Most of them planktonic stage of *Tretomphalus.*
[2] All appeared to be *Mysinae* sp. Mysids constituted 52.8% of the volume of daytime collections.
[3] Included *Mysinae* sp. and *Sirella* sp., the latter unseen in daylight. Mysids constituted 44.8% of the volume of nighttime collections.

GUT CONTENTS OF THE PLANKTIVOROUS FISHES.—The gut contents of diurnal fishes collected at the same time, and in the same location, as the daytime plankton collections are listed in Table 4, and those from the nocturnal species, which were collected between midnight and first morning light on nights when the plankton were sampled, are listed in Table 5.

Where Currents Were Strong

General Observations

Currents were periodically strong near the passes from the open sea, and here, where patch reefs and other hard substrata typically are covered with living corals, underwater visibility consistently exceeded 20 m.[4] The lagoon floor in these areas generally is coarse, well-sorted sand (a sample of the sediment at the Bogen Island site proved to be about 60% fragments of calcareous algae, *Halimeda* spp., with a density of 1.25 g/ml; grain size in over 80% of this sample was greater than 1 mm).

PLANKTON.—Plankters were noted infrequently during casual diurnal observations where currents were strong. Nevertheless, the mysids so prominent where currents were weak occurred here only in small, inconspicuous swarms that concentrated close in the lee of patch reefs when currents were running. The larger zooplankters, frequently so prominent after dark in weak-current areas, were not noted here in any abundance, although nocturnal observations underwater in this habitat were limited.

FISHES.—During the day planktivorous fishes were especially numerous in these surroundings. Many diurnal species were concentrated here, the more prominent being: the serranid *Mirolabrichthys pascalus,* the lutjanid *Pterocaesio tile,* and the damselfishes *Chromis agilis, C. caerulea, C. lepidolepis, C. margaritifer, Pomacentrus coelestus,* and *Dascyllus reticulatus. Pomacentrus*

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[4] Our concept of strong-current locations does not include those breaks in the interisland reefs where the lagoonward flow of water crossing the reef concentrated and spilled into the lagoon at sometimes exceptionally high velocities. These currents were localized and relatively shallow. Planktivorous fishes present were essentially those of nearby weak-current locations in the lee of these reefs, and although no collections were made here we would not have expected such currents to be rich in zooplankters, for reasons developed in the Discussion.

TABLE 4.—Food habits of diurnal planktivorous fishes from Walt Island, Enewetak Atoll, site of weak currents. The value outside the parentheses is the rank of the item as food of that fish species (based on incidence and volume in diet); of the two values in parentheses, the first is the percent of fish of that species containing the item, the second is the mean percent of the total diet of that fish species represented by the item.

1. *Apogon gracilis* (juveniles) $n = 10$; 17-37, $\bar{x} = 27$ mm SL
2. *Pomacentrus pavo* $n = 6$; 46-65, $\bar{x} = 57.2$ mm SL
3. *P. vaiuli* $n = 6$; 40-51, $\bar{x} = 50$ mm SL
4. *Dascyllus reticulata* $n = 5$; 50-74, $\bar{x} = 63.7$ mm SL
5. *Amblyglyphidodon curacao* $n = 5$, 67-82, $\bar{x} = 74.2$ mm SL
6. *Chromis agilis* $n = 2$; 50-54, $\bar{x} = 52$ mm SL
7. *C. caerulea* $n = 5$; 44-73, $\bar{x} = 58.6$ mm SL
8. *C. margaritifer* $n = 3$; 43-50, $\bar{x} = 46$ mm SL

Categories present	Mean no.[1]	1	2	3	4	5	6	7	8
Plankton.									
Foraminiferans	36.7	—	—	—	—	—	—	—	—
Siphonophores	0.4	—	—	—	—	—	—	—	—
Mollusk larvae	21.0	—	—	—	—	—	—	—	—
Ostracods	5.4	—	—	—	—	—	—	—	—
Calanoids and cyclopoids	[2]30.7	1(100:90)	2(100:16.2)	4(17:2.5)	1(100:62.7)	2(100:23)	1(100:75)	1(100:85.8)	2(100:41.7)
Harpacticoids	0.3	4(20:0.4)	6(17:0.3)	—	—	—	—	—	
Mysids	1,398.7	—	4(17:0.8)	—	5(33:1.0)	—	4(50:6.0)	4(20:1.4)	—
Hyperids	5.0	—	—	—	—	—	—	—	—
Caridean larvae	6.0	—	5(17:0.5)	—	4(67:2.3)	—	—	5(20:1)	—
Reptantian zoea	20.0	—	—	—	—	—	—	—	—
Brachyuran megalops	0.2	—	—	—	—	—	—	—	—
Chaetognaths	1.0	3(40:3.6)	—	—	—	—	—	—	—
Larvaceans	([3])	—	—	—	—	—	—	2(20:8)	4(33:3.3)
Apendicularian larvae	0.1	—	—	6(17:0.5)	—	—	—	—	—
Fish eggs	40.0	2(40:60)	3(67:5.0)	2(50:5.3)	3(67:7.3)	3(40:5.0)	2(100:8.5)	3(60:1.8)	3(67:8.3)
Fish larvae	11.3	—	—	—	—	—	—	—	—
Algal fragments		—	1(100:77.2)	1(100:85)	2(67:15)	1(100:65)	3(50:10.5)	—	1(100:46.7)
Crustacean fragments		—	—	—	(33:17)	—	—	—	—
Gurry		—	—	—	(33:10.0)	(60:7.0)	—	(20:2.0)	—
Benthic:									
Cephalaspidean mollusks		—	—	5(17:1.7)	—	—	—	—	—
Compound ascidians		—	—	3(33:5.0)	—	—	—	—	—

[1] Numbers of plankters (from Table 2) provided only for rough measure of relative abundance.
[2] Calanoids and cyclopoids not separated in gut contents; both occurred in all fish species but calanoids predominated.
[3] Larvaceans not present in plankton collections but in two fish guts.

TABLE 5.—Food habits of nocturnal planktivorous fishes from Walt Island, Enewetak Atoll, site of weak currents. See Table 4 legend for explanation of listed values.

1. *Myripristis pralinus* $n = 10$; 82-124, $\bar{x} = 100$ mm SL
2. *M. violaceus* $n = 11$; 120-168, $\bar{x} = 149$ mm SL
3. *Apogon savayensis* $n = 9$; 50-71, $\bar{x} = 60.7$ mm SL
4. *A. novaeguinae* $n = 10$; 20-42, $\bar{x} = 32.1$ mm SL

Plankton categories present	Mean no.[1]	1	2	3	4
Foraminiferans	337.0	—	—	—	—
Siphonophores	2.6	—	—	—	—
Polychaetes[2]	28.3	6(20:5.3)	1(91:45.4)	5(11:5.6)	7(10:5.5)
Mollusk larvae	55.2	—	—	—	—
Pteropods	2.0	—	—	—	—
Squid	0.3	—	10(9:0.5)	—	—
Ostracods	26.4	11(10:0.2)	—	—	—
Calanoids	579.5	[3]1(100:37.0)	[3]5(36:1.4)	[3]6(11:2.2)	1(70:38.3)
Cyclopoids	39.0	—	—	—	—
Harpacticoids	9.3	—	—	—	—
Stomatopod larvae	1.0	—	4(18:4)	7(11:1.7)	—
Mysids	3,031.8	2(80:17.5)	3(56:9.7)	2(67:26.1)	5(30:4)
Cumaceans	12.4	—	—	—	—
Isopods	5.3	7(20:1.5)	—	8(11:1.1)	—
Tanaids	(4)	10(10:0.5)	—	—	9(10:1)
Hyperids	17.8	—	—	—	—
Gammarids	23.2	8(20:1)	11(9:0.2)	—	10(10:0.3)
Caridean larvae	504.2	—	—	9(11:0.6)	2(70:18.2)
Caridean adults and juveniles	20.0	5(50:7.0)	8(9:3.7)	4(44:7.8)	3(30:16.0)
Reptantian zoea	629.8	—	—	—	11(10:0.2)
Brachyuran megalops	60.3	3(50:17.3)	2(82:23.1)	1(100:28.3)	6(20:3)
Chaetognaths	92.4	9(10:1)	—	—	—
Larvaceans	0.4	—	—	—	—
Apendicularian larvae	0.4	—	—	—	—
Fish eggs	273.6	—	—	—	8(10:2)
Fish larvae	51.2	4(30:8.2)	6(18:2.7)	3(56:20.6)	4(30:11.5)
Fish adults and juveniles	0.3	—	7(9:4.7)	—	—
Insects	(4)	—	9(27:0.9)	—	—
Algal fragments		—	—	—	—
Crustacean fragments		—	(9:2.3)	(33:6.0)	—
Unidentified fragments		—	(18:1.4)	—	—

[1] Numbers of plankters (from Table 2) provided only for rough measure of relative abundance.

[2] Most polychaetes in guts of fishes were nereid epitokes.

[3] Predominant calanoids in the three larger fish species were *Pleurommama xiphias* and *Euchaeta marina*, which were relatively large (3 to 5 mm).

[4] Tanaids and insects were not present in plankton collections but were in several fish guts. Both are known from plankton collections elsewhere (e.g., Hobson and Chess 1973, 1976).

vaiuli was numerous, but perhaps no more so than where currents were weak (see above), and here too it confined itself to the immediate proximity of the reef.

The nature of the substrate can be important. *Chromis caerulea* and *Dascyllus reticulatus*, for example, swam in tight well-defined aggregations above specific growths of branching coral—particularly large heads of *Pocillopora* spp. (Figure 5A). *Pomacentrus coelestus* generally stationed itself low in the water column above outcroppings of coral rock and rubble, its relation to the substrate much like that of the similarly hued, but deeper-bodied, *P. pavo*. *Chromis agilis*, *C. lepidolepis*, and *C. margaritifer* generally swam in small widespread groups over patch reefs. Compared with their congener *C. caerulea*, they showed less affinity to specific substrata or locations on the reef. Thus *C. caerulea* invariably responded to a human intruder by sheltering among the branches of a large coral head directly below its feeding station (Figure 5B), whereas *C. agilis*, *C. lepidolepis*, and *C. margaritifer* frequently responded to the same stimulus by moving away, and taking shelter in a variety of places only when the stimulus was intensified.

In places where many of these diurnal planktivores were concentrated, a relation was evident between their morphologies and the distances they swam from the reef: those with feeding stations farther from the reef tended more toward cylindrical bodies and deeply incised caudal fins (Figure 6). This generalization proved valid despite exceptions among such deep-bodied forms as *Dascyllus reticulatus* (Figure 7) and *Amblyglyphidodon curacao*, in which the effect of their deeper bodies is even further enhanced by longer fin spines. Thus, for example, 7 *D. reticulatus*, 47

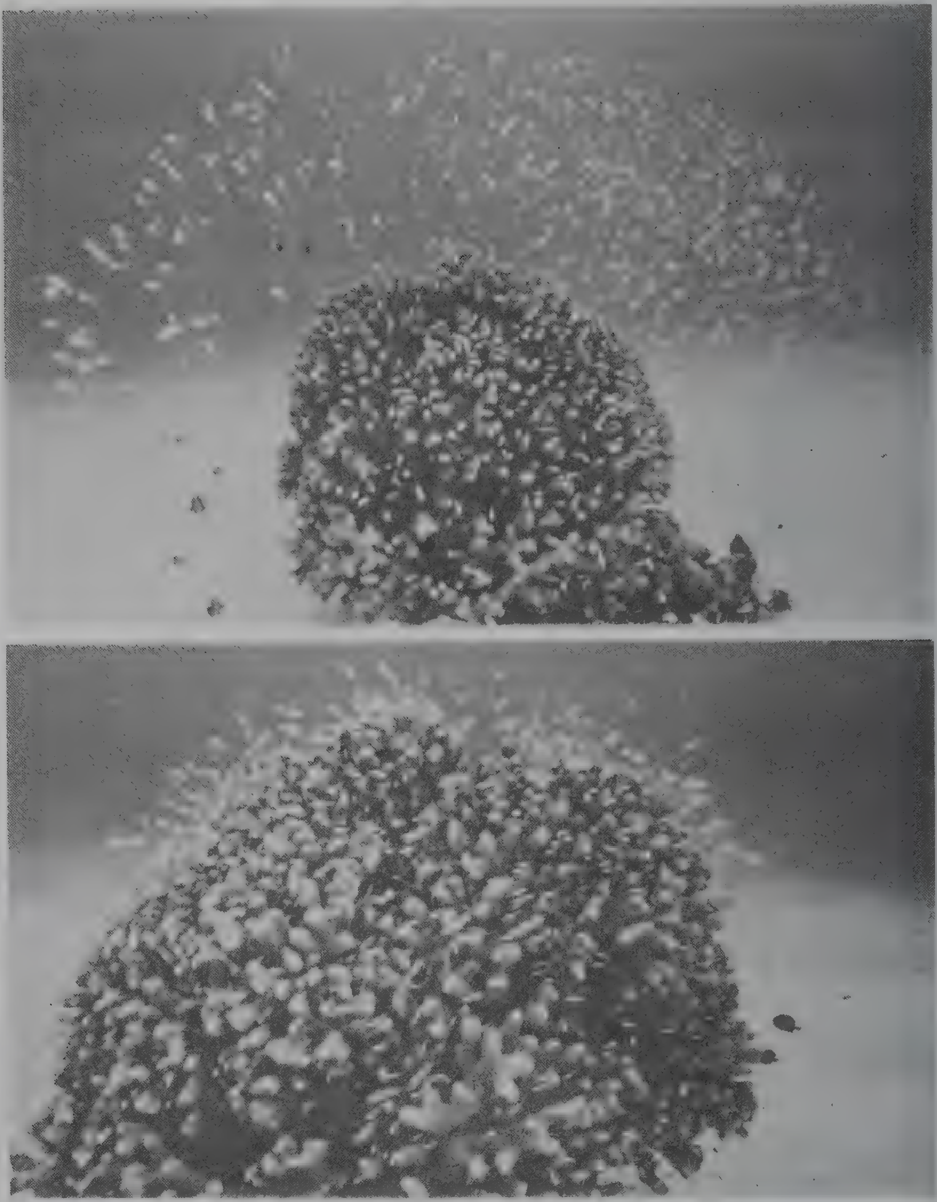

FIGURE 5.—A. *Chromis caerulea*, and a few *Dascyllus reticulatus* (lower left), feeding on plankton above a head of *Pocillopora* at the Bogen Island site. The largest fish are about 70 mm SL; the coral head is about 1.5 m in diameter. B. Upon being threatened, the fish shown in 5A dive to shelter in the interstices of the coral head.

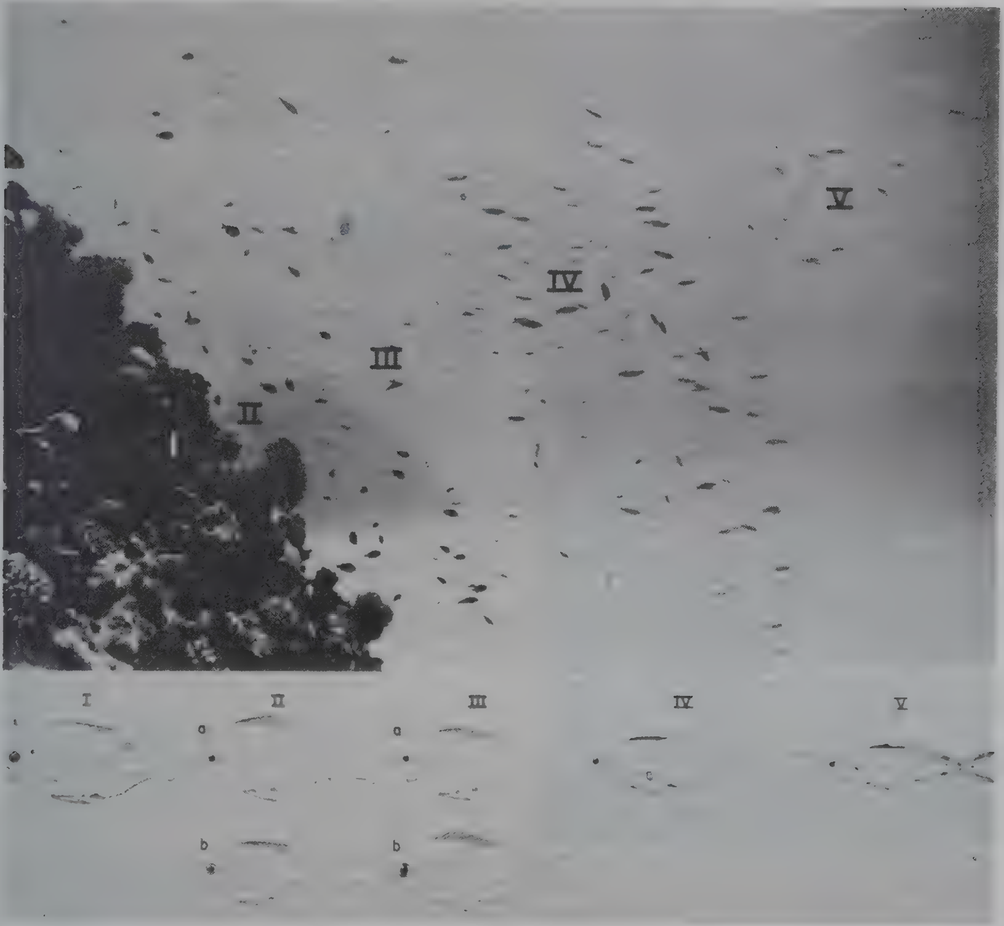

FIGURE 6.—Planktivorous fishes where currents are strong. Major species in each of the zones identified in the photo by roman numerals are illustrated in the appropriate column below the photo (placement based on observations made at the scene). I. *Pomacentrus vaiuli;* II. a, *Chromis agilis,* b, *C. margaritifer;* III. a, *C. caerulea,* b, *C. lepidolepis;* IV. *Mirolabrichthys pascalus;* V. *Pterocaesio tile.*

to 60 mm SL, $\bar{x} = 55.9$, had longest dorsal fin spines that were 20.3 to 23.4%, $\bar{x} = 21.0\%$, of their standard length, whereas these values for 13 individuals of *Chromis* spp. (4 *C. agilis,* 4 *C. caerulea,* and 5 *C. lepidolepis*), 52 to 70 mm SL, $\bar{x} = 59.4$, were 12.3 to 16.1%, $\bar{x} = 15.3\%$. The significance of these data becomes clear when possible selective values of both fusiform and deep-bodied morphologies in planktivorous fishes are treated in the Discussion.

Although most diurnal planktivorous fishes favored conditions associated with current, the strongest currents observed at this site, approximately 1 m/s, clearly exceeded optimum velocities. When such currents flowed, most of the smaller planktivores were close to the reef, many of them concentrated in the lee, and their feeding rates had noticeably declined.

In comparison to the great numbers of adult diurnal planktivores in these surroundings, the nocturnal planktivores were sparse. Although observations underwater in this habitat at night were limited, only a relatively few individuals of

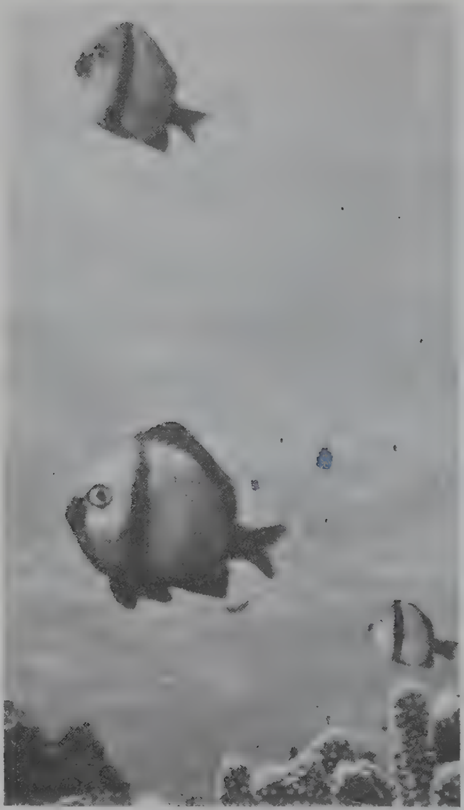

FIGURE 7.—*Dascyllus reticulatus* illustrates the tendency toward a deep body in certain diurnal planktivores that is in contrast to the tendency toward a more cylindrical body in many others.

Myripristis spp. and *Apogon* spp. were seen. Furthermore, during extensive daytime observations here we failed to note the dense concentrations of these and other nocturnal fishes in diurnal shelters that were widespread and obvious where currents were weak.

Samples From Bogen Island

PLANKTON.—The major materials taken in the net at the Bogen Island site of strong tidal currents were zooplankters and algae fragments (Table 6). To facilitate comparisons with collections from the weak-current site, all volumes are standardized to a 5-min collection. The table lists volumes of plankters actually collected, as well as volumes adjusted to the standard relative net speed of 28 cm/s (the net speed at the weak-current site).

TABLE 6.—Composition of plankton in 6 day and 6 night collections at Bogen Island, Enewetak Atoll, site of strong currents.[1]

Items	Zooplankters	Algae fragments	Totals
Day collections:			
Mean vol (ml):			
Collected	2.8	5.7	8.5
Adjusted	1.2	2.7	3.9
Mean % of total vol	32.3	67.7	100.0
Night collections:			
Mean vol (ml):			
Collected	7.3	1.9	9.2
Adjusted	3.9	1.0	4.9
Mean % of total vol	78.8	21.2	100.0

[1] Currents during diurnal collections: 32 to 90 cm/s, $\bar{x}$ = 57; currents during nocturnal collections: 15 to 83 cm/s, $\bar{x}$ = 45

The zooplankters collected at Bogen Island, grouped by major taxonomic categories and with data pooled from the three collection depths (surface, middepths, and near bottom), are listed in Table 7. For the reasons given above concerning volumes, the table lists numbers of plankters actually collected and numbers adjusted to the standard relative net speed. Additional data on calanoid copepods (Table 8) are presented to support certain points developed in the Discussion.

Possibly zooplankters attempting to hold station above precise points on the sea floor would be sampled less effectively by the stationary net during the slower currents sampled at Bogen Island than by the moving net used at Walt Island. We discount this possibility as a significant source of error, however, because we did not see such organisms during our underwater observations of the operation, or when examining collections that sampled a wide range of current velocities.

GUT CONTENTS OF THE DIURNAL PLANKTIVOROUS FISHES.—The gut contents of diurnal fishes collected at the same time, and in the same location, as the daytime plankton collections are listed in Table 9. Only a relatively few nocturnal planktivores (all of them *Myripristis* spp. and *Apogon* spp.) were seen during the limited observations in this habitat after dark, and none were sampled.

DISCUSSION

We were unable to intensively sample more than two stations in the limited time available to us at Enewetak. Nevertheless, data collected at these two sites under a variety of conditions,

TABLE 7.—Occurrence, number (actual and adjusted for current velocity), and size of zooplankters collected day and night at Bogen Island, Enewetak Atoll, site of strong currents.

	Day (n = 6)				Night (n = 6)			
Plankton categories present	Size (mm)	Percent occurrence	Mean no. (collected)	Mean mo. (adjusted)	Size (mm)	Percent occurrence	Mean no. (collected)	Mean no. (adjusted)
Foraminiferans[1]	0.3-1.0	100	56.3	27.7	0.3-2	100	558.7	346.4
Siphonophores	4.0	17	0.6	0.3	4-8	50	5.7	3.5
Polychaetes	3.0	17	0.6	0.3	3-20	100	6.9	4.3
Mollusk larvae	0.5-2.0	100	11.1	5.4	0.5-2	100	31.1	19.3
Pteropods	0.5-6.0	100	6.3	3.1	2-12	83	33.7	20.9
Squid	—	0	0.0	0.0	3-4	50	1.8	1.1
Cladocerons	0.7-1.0	33	0.9	0.4	—	0	0	0
Ostracods	0.5-2.0	100	14.1	6.9	0.5-2	83	107.6	66.7
Calanoid copepods	0.5-4.0	100	1,726.7	846.4	0.5-5.0	100	7,751.1	4,820.1
Cyclopoid copepods	0.5-2.0	100	840.0	411.7	0.5-2.0	100	303.6	188.6
Harpaticoid copepods	0.5-2.0	100	23.0	11.3	0.8-2	67	6.2	3.8
Mysids	2.0	83	6.2	3.0	0.5-7	67	16.2	10.0
Stomatopod larvae	—	0	0	0	20-25	17	0.2	0.1
Cumaceans	—	0	0	0	2	17	0.1	<0.1
Tanaids	2.0	17	0.6	0.3	—	0	0	0
Isopods	—	0	0.0	0.0	1-3	100	57.3	35.5
Hyperid amphipods	0.4-2.0	50	32.2	15.8	0.5-6	100	76.0	47.1
Gammarid amphipods	1.0	17	0.6	0.3	3-4	100	38.4	23.8
Euphausid larvae	0.5-7.0	50	5.0	2.5	0.8-1	33	9.1	5.6
Caridean larvae	1.0-4.0	100	81.2	39.8	1-10	100	386.1	239.4
Caridean adults and juveniles	2.0-6.0	33	2.8	1.4	5-15	83	13.1	8.1
Reptantian zoea	0.5-2.0	100	252.8	123.9	0.5-4	100	509.7	316.0
Brachyuran megalops	1.5	17	0.6	0.3	1-6	100	115.4	71.6
Ophiuroid larvae	2.0	17	0.5	0.3	—	0	0	0
Chaetognaths	2.0-15.0	100	75.3	36.9	3-55	100	440.0	272.8
Larvaceans	1.0-3.0	100	25.3	12.4	2-4	100	87.4	54.2
Salps	—	0	0	0	(?)	17	1.1	0.7
Fish eggs	0.5-2.0	100	732.2	358.8	1-2	100	3,785.6	2,347.1
Fish larvae	2.0-6.0	50	6.6	3.2	[2]3-90	100	46.6	28.9

[1] Most of them planktonic stage of *Tretomphalus*.
[2] A 90-mm leptocephalus larva.

TABLE 8.—Size distribution of calanoid copepods, day and night, at Bogen Island, Enewetak Atoll, site of strong currents.

Size (mm)	Midday (n = 6)		Night (n = 6)	
	Percent	Mean no.[1]	Percent	Mean no.[1]
>3-4	0	0	5	[2]246.7
>2-3	3	[3]26.2	25	[4]1,203.6
>1-2	54	[5]453.7	60	[6]2,888.6
<1	43	366.5	10	481.4

[1] Numbers from collections in varying currents adjusted for equivalence to collections from the Walt Island site.
[2] Including *Euchaeta marina*.
[3] Including *Candacia* sp. and *E. marina*.
[4] Including *Candacia* sp., *E. marina*, *Neocalanus* sp., and *Undinula vulgaris*.
[5] Including *Acartia* sp. and *Euchaeta* sp.
[6] Including *Acartia* sp., *E. marina*, and *Metridia* sp.

supplemented by widespread observations elsewhere, permit a synthesis that we hope stimulates needed additional study. The following discussion pertains to adults of the planktivorous fishes and to plankters collected by our 0.333-mm mesh meter net. All food items found in the fish guts occurred in these plankton collections, so the combined assemblage can be considered a trophic unit. The situation described from these data, however, may not apply to smaller individuals. Limited data, including that from *Apogon gracilis*, the only planktivore studied as an early juvenile, suggest that the smaller plankters which passed through our net, and their predators among juvenile and larval fishes, may follow significantly different patterns (see Miscellaneous Considerations below).

Diurnal Relationships

Probably diurnal planktivores concentrated where strong tidal currents flowed into the lagoon through the passes because these waters were rich in zooplankters, particularly calanoid copepods (Table 7). We presume that at least many of these were oceanic zooplankters carried to within reach of inflowing tidal currents on the eastern side of the atoll by the westward flowing North Equatorial Current—a phenomenon amplified by the trade winds. In addition, some of the materials carried from the lagoon on the preceding ebb tide probably return. Although this outflow is minimal on the windward side of the atoll, at least during the trade-wind season (see von Arx 1948), it probably contains significant amounts of certain kinds of organisms. Gerber and Marshall (1974) noted that the waters of the Enewetak lagoon are much richer in zooplankton than the surrounding ocean. Describing the same condition at Bikini, Johnson (1949) stated: "Much of the oceanic plankton

TABLE 9.—Food habits of diurnal planktivorous fishes from Bogen Island, Enewetak Atoll, site of strong currents. See Table 4 legend for explanation of listed values.

1. *Mirolabrichthys pascalus* $n = 10$; 62-98, $\bar{x} = 79$ mm SL
2. *Pterocaesio tile* $n = 5$; 160-195, $\bar{x} = 174.4$ mm SL
3. *Dascyllus reticulatus* $n = 10$; 50-68, $\bar{x} = 59.6$ mm SL
4. *Chromis agilis* $n = 10$; 54-67, $\bar{x} = 62.1$ mm SL
5. *C. carulea* $n = 9$; 60-77, $\bar{x} = 67.7$ mm SL
6. *Chromis lepidolepis* $n = 9$; 45-67, $\bar{x} = 55.1$ mm SL
7. *C. margaritifer* $n = 10$; 47-55, $\bar{x} = 50.7$ mm SL
8. *Pomacentrus coelestus* $n = 8$; 37-63, $\bar{x} = 50.6$ mm SL
9. *P. vaiuli* $n = 5$; 45-56, $\bar{x} = 52.6$ mm SL

Plankton categories present	Mean no. (from Table 2)[1]	1	2	3	4	5	6	7	8	9
Foraminiferans	27.7	—	—	9(10:0.1)	—	—	—	—	—	—
Siphonophores	0.3	—	—	—	—	—	—	—	—	—
Polychaetes	0.3	—	—	—	—	—	—	—	5(25:1.1)	—
Mollusk larvae	5.4	—	—	—	—	—	—	—	—	—
Pteropods	3.1	—	—	—	—	—	—	—	—	—
Cladocerans	0.4	—	—	10(10:0.1)	—	—	—	—	—	—
Ostracods	6.9	—	—	—	—	—	—	—	—	—
Calanoids and cyclopoids[2]	419.5	1(100:70.4)	1(100:80.7)	3(100:18.9)	2(100:33.6)	1(100:61.1)	1(100:43)	3(100:11.8)	1(88:33.5)	2(80:6.2)
Harpacticoids	11.3	8(10:0.8)	—	8(20:0.6)	5(20:0.2)	5(11:0.6)	5(11:0.6)	—	7(13:0.3)	—
Mysids	3.0	—	—	—	—	—	—	—	—	—
Tanaids	0.3	—	—	—	—	—	—	—	—	—
Hyperids	15.8	9(10:0.2)	—	—	—	—	—	—	—	—
Gammarids	0.3	—	—	—	—	—	—	—	—	—
Euphausid larvae	2.5	—	—	—	—	—	—	—	—	—
Caridean larvae	39.8	2(50:20.4)	2(80:6.0)	5(20:1.3)	4(30:0.7)	5(11:1.1)	4(22:2.6)	4(40:1.2)	4(50:4.3)	—
Caridean adults and juveniles	1.4	—	—	—	—	—	—	—	—	—
Reptantian zoea	123.9	3(50:2)	3(20:0.8)	7(20:0.7)	—	4(11:1.3)	—	—	—	—
Brachyuran megalops	0.3	—	—	—	—	—	—	—	—	—
Ophiuroid larvae	0.3	—	—	—	—	—	—	—	—	—
Chaetognaths	36.9	7(20:0.7)	4(20:0.4)	—	—	—	—	—	—	—
Larvaceans	12.4	6(20:1.2)	—	1(100:40.9)	1(100:49.6)	2(67:17.8)	3(67:20.4)	1(100:61.2)	—	—
Apendicularian larvae[3]	0.0	—	—	6(10:2)	—	—	—	5(10:0.5)	—	—
Fish eggs	732.2	4(30:2.5)	5(20:0.2)	4(90:7.7)	3(100:8)	3(78:12.6)	2(89:20)	2(100:24.1)	2(100:26.3)	3(80:5)
Fish larvae	6.6	5(20:1.5)	—	—	—	—	6(11:0.6)	—	6(13:0.4)	—
Fecal pellets			—	—	7(10:0.3)	—	—	—	—	—
Algal fragments			—	2(90:21.2)	6(20:0.2)	—	—	6(10:0.2)	3(75:23.9)	1(100:84.8)
Crustacean fragments		—	—	(30:0.8)	—	—	—	—	(13:0.6)	—
Unidentified fragments		—	(40:5.0)	(20:5.7)	—	—	—	—	(33:8.3)	—
Gurry		—	—	—	(50:7.4)	(33:5.5)	(44:12.8)	(20:1.0)	(13:1.3)	(20:4.0)

[1] Numbers of plankters (adjusted values from Table 7) provided only for rough measure of relative abundance.
[2] Calanoids and cyclopoids not separated in gut contents; both occurred in all fish species, but calanoids predominated.
[3] Apendicularian larvae not present in plankton collection, but in two fish guts.

swept into the lagoon thrives there and becomes concentrated so that the average concentration per cubic meter of the eleven most common animal groups is about four times higher than outside." In addition, by the time the incoming current passed our Bogen Island station it presumably had picked up lagoon materials upstream, so its contents probably were of diverse origin.

Of course, currents in themselves enhance the planktivorous habit because planktivores holding station above a reef receive more plankters in currents than in equally rich waters without currents. Most of these fishes, however, take shelter by the time a current reaches 1 m/s, so that optimal velocities are somewhat below this. As the current increases, the advantage of receiving more plankters is progressively outweighed by the difficulty of holding station (as was pointed out for *Chromis punctipinnis* in California by Hobson and Chess 1976).

The relatively few adult diurnal planktivores that foraged where currents were weak probably owed their low numbers to the lack there during the day of calanoids and other zooplankters suitable as prey (Table 2). The many zooplankters that tidal currents carried to planktivores elsewhere were unavailable to fishes here, and those taken as prey or otherwise lost were not quickly replaced. Although the volume of zooplankters collected at the weak-current site by day (Table 1) actually exceeded the volume at the strong-current site (Table 6), it consisted largely of swarming mysids (Table 2) which are local residents seemingly unavailable as prey to diurnal planktivores (possibly for reasons discussed below under Miscellaneous Considerations). The strong-current site was in fact much richer in copepods, caridean larvae, larvaceans, and fish eggs—the major prey of the diurnal planktivores (compare Tables 2 and 7).

Locations in the lee of reefs, however, can be rich in drifting debris from these reefs (Gerber and Marshall 1974). This situation existed at the Walt Island site, where *Pomacentrus pavo* and *P. vaiuli*, the most numerous diurnal planktivores there, subsisted largely on algal fragments. Furthermore, the only other diurnal planktivores numerous in weak-current areas, *Amblyglyphidodon curacao* and *Dascyllus reticulatus*, demonstrated a capacity to utilize algae even though both species are largely carnivorous. Gerber and Marshall (1974), too, found that *D. reticulatus* fed on algal fragments when zooplankters were sparse. Obviously, the capacity to utilize algae as food is highly adaptive for planktivorous fishes that would live where drift from a reef is rich in algal fragments, though relatively poor in zooplankters (Table 1).

Despite the adaptiveness of herbivory to planktivores under these circumstances, most of the fishes studied by us were strictly, or predominantly, carnivores. Drifting algal fragments were plentiful in nearly all nearshore habitats, but where zooplankters were also numerous the algae were insignificant in the diets of most planktivores. To be sure, certain species capitalized on drifting algae even where zooplankters were numerous. For example, *P. vaiuli*, which we frequently observed plucking items from the water column, was herbivorous and numerous at the zooplankton-rich Bogen Island site, just as it was at the zooplankton-poor Walt Island site. And *P. coelestus*, which may have replaced *P. pavo* where currents were strong, fed heavily on algal fragments where zooplankters were readily accessible. Yet the pattern is clear—zooplankters were favored by most. Generally *Chromis* spp. have been reported as strictly carnivores even where other planktivorous pomacentrids fed substantially on drifting algae (e.g., in the Marshall Islands by Hiatt and Strasburg 1960; in the West Indies by Randall 1967; and in Hawaii by Hobson 1974). Nevertheless, species of *Chromis* display some capacity to accept algal fragments, as we found in *C. margaritifer* and Gerber and Marshall (1974) found in *C. caerulea*. Thus, where waters are rich in reef debris but poor in zooplankters, we should expect to find *Chromis* spp. in relatively low numbers, just as we did at Walt Island. On the other hand, *Mirolabrichthys pascalus* (a serranid) and *Pterocaesio tile* (a lutjanid) are members of strictly carnivorous families, a fact that probably limits them to places adequately supplied with zooplankters. This view finds support from Gerber and Marshall (1974), who reported that *M. pascales* (as *M. tuka*) and *P. tile* fed entirely on zooplankters. They noted the same for *A. curacao*, *C. agilis*, and *C. lepidolepis* but did not indicate where any of these fishes had been collected, nor whether anything but zooplankters had been available to them. This may be important because one of their major stations was in East Channel, where their plankton collections were without algae, and though they found *A. curacao* strictly carnivorous, we found that it fed heavily on algal fragments where zooplankters were in short supply (Table 4). Gerber and Marshall also noted that *P. vaiuli* fed mainly on algal fragments while coocurring pomacentrids concentrated on zooplankters, but concluded from this that the species is a benthic grazer.

Nocturnal Relationships

Nocturnal planktivores probably concentrated where currents were weak because their prey—including polychaetes, large calanoids, mysids, isopods, gammarids, postlarval carideans, and brachyuran megalops—were most numerous there (Table 2). With the probable exception of at least most of the calanoids (see below), most of these zooplankters were local residents that rose into the water column at night after spending the daytime sheltered on or near the sea floor. This pattern has been adequately documented among these groups of organisms from both Atlantic and Pacific Oceans (Emery 1968; Williams and Bynum 1972; Alldredge and King 1977), and its importance in shaping the activities of nocturnal planktivorous fishes has been stressed (Hobson 1968, 1972, 1974; Hobson and Chess 1976). Food-habit studies have shown that these groups include the major prey of apogonids, holocentrids, and other tropical nocturnal planktivores (Atlantic Ocean: Randall 1967; Indian Ocean: Vivien 1973, 1975; and Pacific Ocean: Hobson 1974).

Only a relatively few nocturnal planktivorous fishes occurred where currents were strong, probably because prey suitable to them were relatively scarce there (Table 7). Many of the organisms on which these fishes feed most likely find conditions in places with strong currents adverse. For example, those nocturnal zooplankters that return each morning to shelter in specific habitats would likely be transported to foreign surroundings should they encounter strong currents while in the water column. The mysids, which include some of the strongest swimmers, probably cannot hold station in currents much over 15 cm/s (based on the maximum swimming speeds of several species: Steven 1961; Clutter 1969) and currents at the Bogen Island station regularly exceeded this sixfold. Organisms that need to spend only a few hours in the water column each night might time their emergence to avoid currents, as pointed out by Alldredge and King (1977), but probably even these would find it advantageous to live without this complex timing problem. Furthermore, many of these nocturnal forms rest in sediments by day (Hobson and Chess 1976; Alldredge and King 1977) and might find the coarse, unstable sand characteristic of strong-current areas unfavorable.

Only part of the increased numbers of zooplankters at night were suitable prey of the nocturnal planktivores. These were individuals more than about 2 mm long, which predominated among the nocturnal visitors at the weak-current site but which were a much smaller segment of the zooplankters that appeared after dark at the strong-current site. Among calanoids, for example, only individuals longer than 2 mm (mostly *Euchaeta marina*, *Pleurommama xiphias*, and *Undinula vulgaris*) were important prey of such larger nocturnal planktivores as *Myripristis* spp., and while these larger calanoids were never seen or collected by us at the weak-current site during the day, they were more numerous than the smaller ones at that station after dark (Table 3). On the other hand, most of the dramatic increase in calanoids at the strong-current site involved only slightly larger individuals of essentially the same species that were there by day, including *Acartia* sp., *Candacia* sp., and *E. marina* (Table 8), and these were largely unexploited by nocturnal planktivores. At 3 mm or less, the majority may be too small to be taken by the relatively large mouths of most of the nocturnal fishes considered here (see Hobson and Chess 1976), although they were important prey of some of the smaller species, such as *Apogon novaeguinae*.

The daytime location of the many calanoids which appear above the reefs at night remains in question. Our nearshore plankton collections in southern California (Hobson and Chess 1976) showed far less increase in calanoids after dark, and we concluded they were in the nearshore water column day and night. But the dramatic increase in calanoids nearshore after dark at Enewetak suggests a different situation. We recognize one or a combination of two possibilities: 1) that some calanoids reside under shelter on the sea floor by day, and join the plankton at night, or 2) that some calanoids reside elsewhere by day, and migrate, or are transported, to the nearshore waters only after dark. There is evidence for both possibilities. The large calanoids that swarmed around our lights shortly after last evening light (but not taken in our collections) could not have traveled far. Alldredge and King (1977) reported calanoids emerging at night from nearshore benthic substrata on the Great Barrier Reef in numbers that could readily account for the increase in calanoids we observed after dark at

Enewetak; but there may be a problem with Alldredge and King's sampling technique. Their samples were taken with Plexiglas traps that rested on the bottom and collected zooplankters that rose into the water column at night; however, there were gaps between the rigid lower edges of these traps and irregularities on the sea floor. Conceivably, as Alldredge and King themselves recognized, the samples could have included swimming organisms from the base of the surrounding water column that entered the traps through these gaps. These collections need to be repeated with this possibility for error eliminated. While it would be surprising if the numbers of calanoids they collected had actually entered the traps through these gaps, we are concerned that the only calanoid identified in their samples, *Acartia* spp. (listed as cyclopoids), are of a genus known to include species that are exceedingly numerous in the water column during both day and night (e.g., Emery 1968; Hobson and Chess 1976). We would expect organisms that live in the substrate by day to have morphological features reflecting this habit that distinguish them from holoplanktonic relatives at the generic level or higher. So although there may have been nearshore residents among the calanoids whose numbers sharply increased after dark at Enewetak, we believe that at least most of them, especially the larger ones, appeared following regular movements from deeper water.

The calanoids that visited the nearshore waters after dark seemed to be part of a nocturnal move shoreward made by many zooplankters, including chaetognaths and larval fishes. Because each of our primary collecting sites probably received nocturnal visitors from different sources, the two are discussed separately.

Walt Island

Perhaps some of the nocturnal plankters that visited the weak-current site were carried from the open sea by the turbulent flow of water that crossed the interisland reef at higher tides, but this would have been a hazardous transit for most zooplankters, and we doubt that significant numbers came this way. If many had come by this incidental route, at least some would still have been there at daybreak—probably somewhat disoriented in these foreign surroundings. But they were always gone by early morning twilight, suggesting they followed a well-established pattern with consistent and predictable arrivals and departures.

Probably most of the nocturnal plankters that visited Walt Island came from the deeper waters of the lagoon, moving over the lagoon's shallow periphery as part of a regular nocturnal rise into the surface waters. The general rise of zooplankters at night in lagoons of the Marshall Islands has been documented (at Bikini by Johnson 1949; and at Majuro by Hobson and Chess 1973). It has also been noted that by day the midlagoon is much richer in zooplankters than is the shallow periphery (Gerber and Marshall 1974), but a shoreward movement among zooplankters at night would reduce this difference between the two regions. Probably it is widespread that zooplankters rising from the depths at night spread out over shallow water near shore. At Kona, Hawaii, where great depths lie adjacent to a coastal shelf (see Hobson 1974), one of us (E. Hobson) often observed myctophids (lanternfishes), and other deep-water forms, in <5 m of water close to shore after dark (unpubl. obs.).

Swimming to the Walt Island site from the deeper water of the lagoon would usually entail moving against the drift from the reef. Although comparatively weak, this current would nevertheless obstruct small or weak-swimming forms. The nocturnal shoreward movement of zooplankters at this location, then, would favor the larger, stronger swimming components of the plankton—forms like chaetognaths, larval fishes, and the larger calanoids. Likely for this reason most of the calanoids among the increased numbers of zooplankters at Walt Island were >2 mm (Table 3), whereas at Bogen Island, where zooplankters were carried by currents, most of a much greater number were 1 to 2 mm long (Table 8). Distinction between the two locations is important because it is the larger zooplankters that were important prey of the nocturnal planktivores. Of course, the upcurrent swim from deeper water would take even the most mobile zooplankters some time. Thus, it is significant that larger calanoids were absent in the plankton collections made at Walt Island 1 h after last evening light, but were numerous in the collections made here at midnight and later (Table 3).

Bogen Island

We presume that most of the zooplankton collected in the flooding tidal currents at Bogen Island had been carried in through East Channel from outside the lagoon—just as during the day. The greatly increased numbers at night probably followed a general rise of zooplankton toward the surface waters in the open sea. Some of these zooplankters were larger than any that were present by day, but such forms represented a lesser proportion of the nocturnal plankton here than they did at the weak-current site. Presumably the collections also included lagoon organisms from upstream, but we would expect these to be relatively few because the entrance to East Channel is only about 1.2 km away (Figure 1). Although the incoming tidal currents probably carried materials that had been transported from the lagoon on earlier ebb tides, we would not expect many of the larger mobile organisms to be among them. Most large mobile forms, it would seem, could avoid being transported from the lagoon by the comparatively weak outgoing currents. But certainly the incoming tide could be returning substantial numbers of passive drifters, like fish eggs and algal fragments, in addition to forms like the smaller calanoids. In any event, we can understand the relative scarcity in the flooding tidal currents of the relatively large nearshore residents (e.g., polychaetes, mysids, and postlarval carideans) that are so important in the diets of nocturnal planktivores.

Probably at least some zooplankters from the deeper waters of the lagoon visited the Bogen Island site at night during periods between flooding tides, but we made no collections at these times. Nevertheless, it would seem that the impact of such forms on the area would be limited, considering how long it takes them to travel without benefit of transport by current, and the fact that a flooding tide sweeps through here during much of most nights.

Miscellaneous Topics

The Nocturnal Increase in Fish Eggs

Planktonic fish eggs represent a special case. Unlike most other zooplankters, which are mobile forms that strongly influence their own distributions, fish eggs are passive drifters that are quickly carried from where they are released if there is any current. Presumably their relative numbers in the water column closely follow the incidence of their release by fishes on the reefs below, and certainly the circumstances of this release have been strongly influenced by the threat from predators that abound over the nearshore reefs. Planktonic fish eggs were a major food of diurnal planktivores (Tables 4, 9) but, despite an almost sevenfold increase in numbers at night (Tables 2, 7), they were insignificant in the diets of nocturnal planktivores (Table 5). Clearly these largely transparent eggs are relatively safe from predatory fishes after dark, probably because they are then invisible. Thus, it would be highly adaptive for reef fishes to release planktonic eggs late in the day, or early in the night, when the eggs have maximum time for dispersing in the dark, relatively free of threat from planktivorous reef fishes.

Possible Influences of Water Depth and Size

Among the promising topics we lacked time to pursue during our short stay at Enewetak were ways that water depths, and the sizes of interacting fishes and zooplankters, may influence trophic relationships.

We believe that the difference in water depth between our primary collecting sites (7 vs. 13 m) did not significantly influence our findings, especially as the deeper station was well away from the deep part of the lagoon (Figure 1)—farther, in fact, than the shallower station. It was apparent to us, nevertheless, that water depth in the lagoon can, directly or indirectly, influence fish-zooplankton interactions. Obviously both fishes and zooplankters are physically limited in extreme shallows, especially in turbulent waters above shallow reefs. But probably the major depth-related influence stems from the general tendency of lagoon zooplankters to seek deeper water during the day (e.g., Johnson 1949; Hobson and Chess 1973)—a tendency that apparently increases with size. We suggest above that many of the larger zooplankters active above the nearshore shelf at night were in the deeper lagoon waters by day, when the water column of the nearshore shelf was largely without such forms. Perhaps the concentrations of planktivores along the outer edge of the nearshore shelf during the day were in contact with the fringe of these deep zooplankton populations.

This leads to a possible influence related to size. Very small zooplankters (those passing through the mesh of our net, and so unrepresented in the collections), and their predators among juvenile and larval fishes, may follow patterns significantly different from patterns followed by the larger forms studied here. The zooplankters descending into the depths by day tend to be the larger individuals, so we wonder where the very small ones are located. In sharp contrast to the relatively few adult planktivores active in weak-current areas of the nearshore shelf by day, large numbers of juvenile and larval fishes (Figure 4) clearly found planktonic food abundant. It may be that very small zooplankters, unsampled by our net and too small to be taken by most adult planktivores, remain numerous in shallow weak-current areas during the day.

Mysids as Prey During the Day

It is striking that when mysids swarm in dense numbers near many reefs during the day they are relatively unimportant as prey of the major planktivorous fishes. They seem to escape the interest not only of diurnal planktivores, but also of the many nocturnal planktivores (e.g., *Myripristis* spp.) that hover within easy reach close among the coral.

To be sure, a number of the fishes we studied took some of these mysids by day. *Chromis caerulea, C. agilis, Dascyllus reticulatus,* and *Pomacentrus pavo* included mysids as minor components of their diet at the weak-current site. Furthermore, Hiatt and Strasburg (1960) reported that *C. atripectoralis* preyed significantly on mysids. But considering the preponderance of mysids in the water column at so many places during the day, these fishes took only token numbers.

Probably the relatively large size of the mysids is important in this context. The evolution of feeding morphologies in diurnal planktivores appears to have been determined by strong selective pressures to take tiny prey (Davis and Birdsong 1973; Hobson and Chess 1976). Significantly, most of the zooplankters taken by these fishes (e.g., copepods, larvaceans, and fish eggs) were <2 mm long, and the size range of mysids that swarmed around these reefs in daylight was 2 to 8 mm (Tables 2, 7). In reporting a similar situation in the tropical Atlantic Ocean, Emery (1968) speculated that planktivorous pomacentrids fail to prey on swarming mysids because normally these fishes feed on smaller prey.

The failure of *Myripristis* spp. and other large-mouthed nocturnal planktivores to exploit this diurnal resource cannot be attributed to the size of the mysids, however, because these fishes find the same mysids major prey at night. Apparently the nocturnal fishes simply do not react to these readily accessible mysids as prey during daylight. In warm-temperature waters of southern California the large juvenile olive rockfish, *Sebastes serranoides,* feeds primarily on zooplankters after dark, but during the day sometimes preys on mysids that are within reach of the rockfish where it hovers in relatively inactive diurnal schools (Hobson and Chess 1976). However, predominantly nocturnal habits seem to be characteristic of the olive rockfish only during its large juvenile stage—both before and after this stage it feeds mainly by day (Hobson and Chess 1976). Therefore, even at that time of its life when the olive rockfish feeds primarily at night, we should not expect it to be as strongly nocturnal as *Myripristis* spp. and the other more specialized nocturnal forms that ignore mysids by day at Enewetak.

Possibly swarming mysids are protected from predators by the nature of their aggregations. Emery (1968) noted that mysid swarms respond to predators just as fish schools do. The analogy can be expanded. Like these nocturnal mysids, many nocturnal fishes congregate in dense numbers above the reef during the day, and at this time they too are relatively undisturbed by the many predators at large in the same area (Hobson 1965, 1968). It is widely believed that fishes are less vulnerable to predators when they aggregate (e.g., Bowen 1931; Springer 1957; Brock and Riffenburgh 1960; Manteifel and Radakov 1961; Williams 1964). Of the many theories that would explain this circumstance, we favor the existence of a confusion effect, as advocated by Allen (1920) and others. This theory suggests that visually orienting predators which select individual prey have trouble singling out a target among the many alternatives they confront in an aggregation. That mysids achieve some safety from predators by aggregating is further supported by the experiments of Welty (1934), who found that goldfish, *Carassius auratus,* consumed fewer daphnia when these prey were concentrated. (These comments apply as well to the relative lack of diurnal predation on larval fishes, which, in their dense schools close to the reef, resembled swarming mysids.)

Planktivore Morphology and Their Distance From the Reef

It was suggested earlier (Hobson 1974) that in their tendencies toward more fusiform bodies and deeply incised caudal fins, diurnal planktivores have acquired added speed that is adaptive in quickening their return to reef shelter when threatened. Expanding this suggestion, these features are more developed in planktivores that swim farther from the reef because threats from predators probably increase in more exposed locations. Although morphology that permits faster swimming would also enhance holding station in a current, we believe the major selection pressures shaping these features in planktivores have come from predators.

Despite the obvious adaptiveness of fusiform bodies and of deeply incised caudal fins in many planktivores, the morphologies of certain other highly successful diurnal planktivores have taken the opposite course. For example, among the fishes we studied, *Dascyllus reticulatus* (Figure 7) and *Amblyglyphidodon curacao* are among the deepest bodied of pomacentrids, and yet they range farther into the water column than the species of *Chromis* or *Pomacentrus*. Similarly, the many planktivorous chaetodontids in Hawaii (e.g., species of *Chaetodon* and *Hemitaurichthys*), all deep-bodied forms with truncate caudal fins, are highly successful planktivores that range widely in the water column (Hobson 1974).

We suggest that whereas fusiform bodies increase the chance of eluding predators, deep bodies increase the chance of discouraging predators. The basis of this second suggestion is the fact that piscivores live with the danger of choking on spiny-rayed prey lodged in their pharynx or esophagus. Over the years we have seen many predators in this predicament—often fatally. Piscivores generally swallow their prey head-first, frequently after manipulation to ensure proper orientation. Reasons for not swallowing a spiny-rayed fish tail-first are obvious. Assuming, then, that a prey fish is swallowed head-first, the danger of it becoming lodged in the pharynx or esophagus increases with its depth or width. Thus, predators equipped to take prey from among the variety of planktivores in the water column (where those at a given level tend to be about the same length) would find greater risk ingesting deeper bodied forms, especially those with prominent fin spines. Of course, this advantage of a deep body and prominent spines in thwarting predators extends beyond planktivores; the entire family Chaetodontidae, for example, would benefit (Hobson and Chave 1972).

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7816

Economic Constraints On Food Production From The Sea

Daniel D. Huppert
U.S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
La Jolla, California

That marine ecological systems are tremendously productive of plant and animal life is an established fact. In assessing the potential for food production from the sea, however, marine scientists have produced quite a range of "estimates" of the sea's productivity. In 1965 Schaefer (1) conservatively estimated that the world fishery production could be increased to 200 million tons "with no radical developments, such as fish farming or far out kinds of fishing gear." This total production was to include all fish, molluscs, and crustaceans supporting traditional fisheries.

Noting that the nutritional value of animal protein is essentially the same whether it comes from the bluefin tuna, the anchovy, or the lowly Antarctic krill, Chapman (2) surmised that any estimate of the sea's potential must assume something about man's tastes and needs. If people need and desire a traditional mix of taste, texture and fragrance, then much of the food must come from the relatively scarce populations of third and fourth-stage carnivores. If, on the other hand, man desires only a balanced mix of amino acids, minerals and vitamins, then food production may rely upon the more abundant lower-stage plants and animals. The potential annual yield of well-balanced, undifferentiated animal protein could, according to Chapman, range up to 2 billion tons. The annual sustainable yield of the more desirable predators would amount to only around 60 million tons.

These estimates refer only to the harvest of wild stocks. More intense cultivation techniques, loosely termed "aquaculture", are estimated to yield over 4 million metric tons worldwide annually (3). Much of this tonnage is derived from fresh and brackish waters. True mariculture is really an infant industry, but Bardach, Ryther and McLarney claim that yields from existing aquaculture installations could increase tenfold over the next three decades if "there were no economic constraints on the upgrading of culture" (3).

All these predictions of physical or technological potential appear somewhat academic in view of the history of world fish catches. World production of fish has leveled off since the post-war boom (see Table I). Whether this is a more-or-less permanent feature of world fisheries is not easy to determine at this early stage. But many of the known, abundant food fish stocks having the "taste, texture and fragrance" to which Western man, at least, has become accustomed, appear to be fully exploited. North Atlantic groundfish stocks have been fully, or nearly-fully exploited for several years (4). It is becoming increasingly clear that the same is true of North Pacific stocks of groundfish and of most northern hemisphere pelagic fish. Certainly, there are several stocks which are relatively lightly fished at present (jack mackerel, anchovies and squid in the Pacific come to mind), and further exploratory fishing in the South Pacific and Indian Ocean could reveal more potential fisheries. Nevertheless, the volume of untapped potential resources is dwindling. The expansion of production of food fish requires that increasingly marginal stocks be exploited or that tastes be altered to accept previously unacceptable fish. It appears that Chapman's estimate of 60 million tons for highly desirable food fish was close to the mark.

Fish caught for reduction to meal and oil accounted for a major part of the expansion in world fish production in the 1960's. Peru, South Africa, Norway and Iceland are responsible for the lion's share of the fish meal

Table I

Total World Fisheries Catches, 1950-1975

(million of metric tons)

Year	Catch	Year	Catch
1950	21..1	1963	48.2
1951	23.5	1964	52.5
1952	25.1	1965	53.3
1953	25.9	1966	56.8
1954	27.9	1967	61.1
1955	28.9	1968	64.3
1956	30.4	1969	62.9
1957	31.5	1970	70.0
1958	33.2	1971	70.9
1959	36.7	1972	66.2
1960	40.0	1973	66.8
1961	43.4	1974	70.5
1962	46.9	1975	69.7

and oil entering world trade, although the United States and Japan produce significant amounts of meat, also. As shown in table II, however, a halt to the expansion in fish caught for reduction paralleled the deceleration in food fish catch. It has been found, at least tentatively, that many of the abundant schooling pelagic fish easily exploited for reduction are either fished to the maximum yield or are only infrequently highly abundant. A few pockets of potential expansion, such as the northern anchovy off the west coast of North America, are well known. But the few hundred thousand tons of annual yield which could be afforded by addition of these under-exploited stocks to the world fisheries would not change the world situation significantly.

Table II

Disposition of World Catch, 1970-1975

Year	1970	1971	1972	1973	1974	1975
	(millions of metric tons)					
Total world catch	70.0	70.9	66.2	66.8	70.5	69.7
For human consumption	43.5	45.4	45.8	48.2	49.5	48.7
Marketed fresh	19.5	20.1	19.8	20.5	21.3	20.7
Freezing	9.7	10.7	11.2	12.5	12.9	12.7
Curing	8.1	8.0	8.0	8.0	8.1	8.1
Canning	6.2	6.6	6.8	6.8	7.2	7.2
For other purposes	26.5	25.5	20.4	18.6	21.0	21.0
Reduction[1]	25.5	19.4	19.4	17.6	20.0	20.0
Miscellaneous	1.0	1.0	1.0	1.0	1.0	1.0

[1] Includes only whole fish destined for the manufacture of oils and meals.

Source: FAO, Yearbook of Fishery Statistics, 1975. (Rome 1976).

In comparison to Schaefer's 200 million ton estimate of annual yield, or to Chapman's 2 billion ton estimate, the limited world production revealed by this casual review of fisheries is disappointing. To some extent the sea's potential may yet succumb to relatively straightforward application of technology, exploration and capital investment. Nevertheless, there are some fundamental economic conditions which must be met before any extensive fishery development efforts can pass unscathed through the crucible of economic reality.

Among the pertinent economic conditions are:

(i) Prices of seafood products must cover all costs of production while being low enough to compete with alternative sources of food; and

(ii) economic waste inherent in over-fishing and overcapitalization must be discouraged in marine fisheries.

These two conditions and likely constraints to their achievement are discussed in the following sections.

Prices and Costs

It is widely recognized that for any productive activity to be economically successful the unit cost of production must be kept below the price at which consumers will buy significant quantities of the product. Individual fishermen and aquaculturists obviously understand this principle and make daily decisions based upon cost and price considerations. The economists' task is to extend and generalize this idea and to apply it to overall supply and demand situations.

Demand analysis begins with the notion that the needs and desires of consumers can be satisfied by a variety of products, and that actual purchases are determined, in part, by the array of prices confronting consumers and by the amount of income available to the consuming public. Thus, given a desire for both an adequate nutritional balance and for special tastes and textures, the typical consumer will allocate his available income over the available foods in a way that is most beneficial to him. Prices have a crucial part to play in the consumer's choices. Obviously, if seafoods, for instance, are more expensive per unit of nutrition and "taste", and if the supplies of alternative foods are expanding at lower prices, then demand for sea food cannot be expected to grow rapidly. The demand for sea food in the United States should be sensitive to price because there are so many red meat and poultry products available in great quantities and at reasonably low prices.

Given this very general conclusion, the retail price indices listed in table III are revealing. During the period 1955-1976, per capita consumption of red meat rose from 128 pounds to 213 pounds; per capita consumption of poultry rose from 27 pounds to 53 pounds; while per capita consumption of fish increased from 10 to 13 pounds. During the same period meat prices have risen at about the same rate as food prices in general; poultry prices have fallen relative to meat and food prices. As a class, fish has become relatively more expensive than the principal alternative high-protein foods. It is probably only the rising trend in per capita income that has helped to maintain the increasing consumption of fish in

Table III

Price Indices for Fish and Competitive Agricultural Products in the United States. (1956-1958 = 100)

	Retail price indices for:				Wholesale price indices for:	
Year	Meat	Poultry	Fish	All food	Soybean meal	U.S. fish meal
1955	87.7	121.5	93.9	94.0	1.11	1.00
1956	84.8	106.5	93.8	94.7	1.00	0.99
1957	94.2	103.8	95.0	97.8	0.92	0.99
1958	104.9	102.6	101.6	101.9	1.09	1.02
1959	101.0	93.5	103.4	100.3	1.10	0.99
1960	99.2	95.0	103.5	101.4	1.03	0.70
1961	100.5	85.8	105.8	102.6	1.29	0.85
1962	102.5	90.7	110.2	103.6	1.29	0.91
1963	100.9	89.3	110.0	105.1	1.41	0.89
1964	99.4	87.3	107.4	106.4	1.35	0.95
1965	106.9	90.0	110.6	108.8	1.39	1.17
1966	116.8	94.9	117.8	114.2	1.63	1.13
1967	113.8	88.9	121.8	115.2	1.49	0.94
1968	116.5	91.7	123.8	119.4	1.51	0.95
1969	126.8	96.9	130.6	125.5	1.45	1.17
1970	133.9	96.4	143.7	132.4	1.54	1.38
1971	132.9	96.9	158.6	136.4	1.51	1.18
1972	147.1	98.2	172.9	142.3	2.04	1.30
1973	183.4	137.7	198.3	162.9	4.63	3.41
1974	186.8	130.7	228.7	186.3	1.74	2.09
1975	202.7	144.4	247.7	202.1	2.41	1.79
1976	202.7	136.9	276.9	208.3	3.16	2.49

the United States. Assuming that the price trend revealed by the retail price index for fish is the result of increasing costs of production relative to those of the other foods, these figures may reflect a relatively poor performance of the U.S. fisheries relative to U.S. agriculture. Another interpretation of the retail price trend is that the fisheries have operated at least cost but have been unable to expand production to meet the increasing demand due to constraints on the available fish stocks. With increasing demand and steady or sluggish supply, prices will rise. With either interpretation, it is clear that the domestic sea food industry is not demonstrating a capability for expanding production in tandem with land-based food industries. Furthermore, because much of the sea food consumed domestically is imported, it may be inferred that our foreign trading partners are subject to the same limitations. Yet the biological potential of the oceans, if we are to believe Chapman (5) and Schaefer (1), has hardly been exhausted. The increasing cost and sluggish supply is probably due to the full or over-exploitation of traditionally important fish stocks, accompanied by the inability of the industry to supplement traditional fisheries with new species or product forms from the unused or under-developed fish stocks. From an economic viewpoint the ocean's potential is well developed.

Available biological productivity does not imply economic productivity unless the biological products are both desired by consumers and cheaply produced. The most stringent economic constraint upon further expansion of food fish harvests appears to be the meager demand for most of the unused species at prices covering the unit production costs and providing a reasonable expectation of profit to the producers.

The market for industrial fishery products is quite similar to that for food fish, but with a twist. Because fish meal and oil enter the production processes for other goods as relatively undifferentiated inputs (i.e. not species-specific nor required to have subtle qualities to be acceptable), the market potential is not so severely constrained by tradition, culture or the biological productivity of popular fish stocks. In the case of fish meal the need for high protein supplements in poultry and livestock feed can be met by vegetable protein meals such as soybean meal. In table III it is indicated that soybean meal prices have risen relative to fish meal prices during the last two decades. Fish meal producers should, therefore, be in a good position to expand production and increasingly encroach upon the markets for high protein meals.

Contrary to this expectation the production of fish meal has shown the same sluggish tendency as has become expected of food fish production. Apparently, the concentrations of pelagic schooling fish (clupeoids, in particular) which can be caught inexpensively (i.e. at a cost of 25-50 dollars per ton) are an increasing rarity. Thus with fishery reduction products, as with food fish, the biological potential of the sea is barely exploited while the economically useful portion of that potential is largely developed. To expand the fisheries for reduction fish into, for example,"trash" bottomfish would cause an increase in the cost of fish meal due to the harvest costs. Higher raw fish costs must be covered by higher final product prices, but prices cannot be much higher if competitiveness is to be maintained. Any technological advances which increase the availability of fish for reduction at current prices would be useful. This applies equally to food fish production. However, technical innovations in our domestic fisheries are as likely to increase the rate of exploitation on existing fully exploited stocks as they are to help broaden the resource base.

Aquaculture may be a solution to this dilemma. By placing the entire process of production (or, at least, more of the process than is encompassed by the traditional fisheries) within the control of men, aquaculture presents us with the opportunity of applying more scientific methods to the food production process. Instead of hunting wild stocks, we establish specific stocks of favored species selected for genetic characteristics which optimize growth, appearance or whatever else promotes economic value. Under controlled conditions mortality is low and growth is fast. The productivity of the feed lot is applied to marine organisms.

There are isolated instances of reasonable success with aquaculture. Paradoxically, very few of the real successes have been developed through the application of Western technological knowhow in recent years. Oyster and mussel culture, salmon and trout rearing, and pond culture of carps and "milkfish" have all been developed over a much longer period than is spanned by the recent science of aquaculture. Infusions of modern scientific methods have undoubtedly helped to overcome problems of disease control and nutrition. This makes possible more physically productive and economically profitable aquaculture projects, but the amount of food fish produced by aquacultural techniques remains relatively meager.

Current developments in aquaculture seem to focus almost entirely upon high-priced products such as the salmonids, shrimp (6), freshwater prawns (7), and delicacies like lobster and abalone. The major reason for this emphasis is clear—the cost constraint on the production of delicacies is much less severe than on the production of staples. Given the high production costs characteristic of developing technologies, it is not surprising that intensive aquaculture techniques should be applied to high-priced species. High prices, however, dictate low volume.

Furthermore, in assessing the potential for food from the sea, it is not clear that the intensive aquacultural techniques will ever be economic enough to compete with agriculture or even to challenge the primitive hunting of fish with vessels. Ultimately, the cost and availability of requisite inputs such as water, coastal land, labor and technical expertise will determine the extent to which aquaculture will become competitive. Unless it is competitive in price, aquaculture will never contribute significantly to the world food supply. Recent studies (8) seem to be pessimistic about the possibility of great strides in the direction of lower cost aquaculture.

Management of Fish Stocks

Although biological productivity, demand for sea food, and harvest costs encompass the main constraints to food from the sea, a different type of impediment to food production is the institutional convention called "common property" or "free access". So long as oceanic fishery resources are open to exploitation by all without restriction, no fisherman competing vigorously to improve his own lot in life has much incentive to control his take of fish. It has long been recognized that the limited biological productivity of any animal population can be severely reduced through over-fishing by competitive fishermen. The power of government has been invoked in many instances to prevent over-fishing, but existing fishery regulations are often economically irrational and are also too limited in scope to deal with international fishery problems. As more of the world's fishery resource comes under the jurisdiction of coastal States, and as more of the oceanic fish stocks of real importance are brought under international management conventions, prospects for conservation of biological productivity will improve. Even if overfishing in the biological sense is prevented, however, the economic costs associated with sea food harvests may be unnecessarily high due to excessive competition for the limited harvests allowed under biologically oriented fishery management.

The importance of economic issues in fishery management was first analysed rigorously by Gordon (9). His conclusions are still appropriate today. Under fishery regulations which do not restrain the number of men and the capital equipment in the fishery, normal economic incentives of competitive fishermen will drive them to apply more and more economic inputs to the fishery until no net economic return can be earned. Thus over-capitalization (that is, investment of excessive amounts of capital equipment) occurs even when over-fishing is prevented. Strictly speaking, over-capitalization does not specifically result in a reduction in harvest of any managed fish stock. The use of enormous amounts of fishing vessels over short fishing seasons can result, however, in a shortage of capital for use in other fishing ventures which would otherwise attract investment funds. Thus the overall impact of free access may be to lessen the world harvest of sea foods.

This economic view of fisheries exploitation has some important ramifications. For one thing, application of advanced technology to ocean fish stocks will not necessarily result in greater harvests but may instead simply lead to more sophisticated and costly over-capitalization. I would certainly hesitate to argue that technological innovation is unimportant to the further development of world fisheries, but I would emphasize that progress would be more rapid if there were institutional safeguards to prevent over-capitalization and to assure at least moderate operating profits in existing fisheries.

Progress toward greater food production would be much facilitated by a re-direction of innovative expertise and capital investment. Rather than emphasizing cost reduction in already heavily-exploited fisheries, investment activities could be devoted to developing new products and new fisheries. Institutions are needed which restrain over-capitalization and encourage the use of the resulting economic profits for fishery development elsewhere. Currently, no such institutions exist. Thus there are as many problems with over-development as there are with under-development in fisheries. The north Atlantic and north Pacific fisheries are coming under increasingly strong harvesting restraints, while potentially profitable fisheries in the Indian Ocean remain underdeveloped largely for lack of investment capital (10). Any field of resource development must reconcile limited availability of capital and innovative expertise with seemingly unlimited opportunities. Under current institutions, the world fisheries must operate under the further constraint that much of the available capital and technology is wasted on duplicate efforts in over-capitalized fisheries. In the long run, the inability of international fishing conventions to deal effectively with the inherent economic inefficiency of common property fisheries may be the most effective constraint to full development of the sea's potential for food production.

That there are economic constraints to the production of food from the sea should come as no surprise. The required relationship of cost to price retards the economic development of many biologically productive fish and shellfish populations due to excessive harvest costs or to lack of consumer demand for reasonable rates of harvest. The same considerations of cost and price limit the current potential for aquacultural developments. And the irrational over-capitalization of many of the world's fisheries squanders an important source of funds for investment and technological development in new fisheries and products. These are real constraints which can prove troublesome to any plans for further rapid development of food from the sea. At the same time, economic constraints should not be accepted with great pessimism, for cautious and deliberate effort to remove or relax the constraints should prove both feasible and beneficial.

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SCHOOL STRUCTURE OF THE SQUID *LOLIGO OPALESCENS*

ANN C. HURLEY[1]

ABSTRACT

The squid *Loligo opalescens* forms schools which are similar in many respects to those of obligate schooling fishes. These schools are marked by parallel orientation of individuals and strong cohesiveness. Laboratory experiments indicate that the main sensory modality regulating schooling is vision. Squid on opposite sides of a clear rigid Plexiglas barrier readily schooled. The structure of schools of six squid depended on size of individuals and was modified by environmental disturbance. Parallel orientation was weaker in schools of smaller squid (ca. 7 cm dorsal mantle length) than it was in larger ones (ca. 12 cm). In the field, *L. opalescens* schools are composed of uniformly sized individuals. Laboratory experiments designed to determine whether this was due to actual size selection were inconclusive, but they did suggest mechanisms which might be important in determining squid position in the school.

Considerable effort has been spent in understanding the schooling behavior of fish in terms of physiological mechanisms and possible survival value and ecological consequences. (See reviews by Radakov 1973 and Shaw 1970, 1978.) Virtually no work has been done on schooling behavior of invertebrates which occur in the same environments as schooling fish. The most evident schooling invertebrates in the pelagic environment are the squid. Squid and fish play very similar ecological roles and the two groups of organisms possess a large number of similarities. (See Packard 1972, for a discussion of convergent evolution.)

Loligo opalescens is common off the west coast of North America with a reported range from Baja California to lat. 55°N (Fields 1965; Bernard 1970). Relatively little is known of the behavior or general ecology of *L. opalescens* in spite of the fact that there is a fishery for this species in California. The fishery is based primarily upon the tendency of squid to spawn in large aggregations in shallow water (McGowan 1954; Fields 1965). Very little is known about the distribution or location of newly hatched squid as well as squid in later stages of life. Attempts to catch the juveniles have often been unsuccessful (Okutani and McGowan 1969) and only recently have attempts been made to catch nonspawning adults. Even though field data are difficult to obtain, it is possible to keep both juvenile (Hurley 1976) and adult *L. opalescens* alive in the laboratory. Schooling in the laboratory was examined to provide insights about the function of schooling in squid.

METHODS

The squid used in the behavioral studies were obtained either by dipnetting them after they had been attracted to an underwater light or by purchasing them from a local bait dealer. In the laboratory, the squid were maintained in a 3-m diameter circular tank with rapidly circulating seawater. They were fed irregularly on small fish (either mosquitofish, *Gambusia affinus*, or goldfish, *Carassius auratus*). Mosquitofish were taken much more readily than were the goldfish. Occasionally, the squid could be trained to take dead food. This was accomplished by first getting them to accept live fish and by then throwing dead fish in along with the live ones. In this manner, the squid could also be coaxed to accept pieces of frozen northern anchovy, *Engraulis mordax*. If the squid were undamaged when they arrived at the laboratory and there was an abundant supply of small fish available, it was relatively easy to keep them for over a month.

Experiments designed to examine various aspects of schooling behavior were run in a 2 × 3 m rectangular Plexiglas[2] tank which was filled to a depth of 0.4 m. The tank was painted flat white and the primary source of lighting (in addition to general room illumination) was provided by

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[1] Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, CA 95039.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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fluorescent lights placed around the perimeter of the tank which shone through the walls. This provided even, diffuse light in the tank. The water in the tank was noncirculating.

Schooling behavior was recorded on Tri-X film using a 35 mm camera with motor drive and a variable setting automatic timer. A mirror was placed above the tank and pictures were taken of the squid by photographing the surface image reflected in the mirror. A black plastic barrier surrounded the experimental tank. A small hole in the barrier allowed observations to be made of the squid without disturbing them. Exact methods, timing of pictures, etc. varied with the experiment and will be described in the appropriate section.

After the films were developed, they were analyzed using a Scientific Data Products data tablet (Graf-Pen) coupled with a PDP 11-45 computer. The data tablet is a set of microphones placed at right angles which record the sound produced by an electrical spark made by a special marking pen. The x and y coordinates of a point were relayed to the computer by pressing the pen down on the tablet at that point. This device allowed the recording of large amounts of squid position data. In each frame, the tip of the tail, the tip of the outstretched arms, and a point midway between the two eyes were recorded for each squid. Other information, such as the position of barriers, was recorded in the same way. Measurements taken from the photographs were subsequently converted to real distances by multiplication by appropriate scale factors.

Students of schooling have examined school geometry both as a two-dimensional system on a horizontal plane (Breder 1959; Williams 1964; John 1964; Hunter 1966, 1968; Van Olst and Hunter 1970) and as a three-dimensional structure (Cullen et al 1965; Symons 1971a, b; Pitcher 1973). Since squid schools do have a three-dimensional structure in nature, a three-dimensional analysis will eventually be necessary to determine all of the structural details of the school. A three-dimensional analysis, however, is much more difficult than a two-dimensional analysis. It was felt that a two-dimensional analysis would suffice to examine certain aspects of squid schooling behavior. In these experiments, the squid were very nearly confined to a two-dimensional plane by the shallow water depth in the experimental tank. Observations of small schools (up to six squid) in a deeper tank (1 m depth) indicated that the two-dimensional structure observed in the experimental tank was not uncommon.

Three indices were chosen to quantify the angular orientation of individuals in a school, the overall shape of the school, and the distance between neighboring individuals in a school. These indices were proposed by Hunter (1966) and he includes a detailed discussion of their properties. The three indices are:

1. Mean separation distance: An average of the horizontal distances separating each squid from every other squid in the school. It is influenced by school shape, distance between neighboring squid, and number of squid in the school. Distances between all possible pairs of squid are measured and these values are averaged. Distance is measured between the two closest points on the midline of the bodies (including outstretched arms) of the two squid.
2. Mean distance to nearest neighbor: An average of distances from each squid in the school to its nearest neighbor. The measurement is made between the two closest points on the midline of the bodies (including outstretched arms) of the two squid. The same measurement is used twice if two squid are closer to each other than to any other squid.
3. Mean angular deviation: This is a measure of the differences in orientation among squid within a school. The heading of each squid is determined and the resultant direction of the school is computed by assigning each squid a value of one and adding the headings vectorally. The mean number of degrees individual squid deviated from this resultant direction of the school was calculated as the index of orientation.

One difference between squid and most of the schooling fish which have been studied is that squid readily swim both forward and backward. Thus, a squid with an orientation that was 180° out of phase with the rest of the school might still be swimming with the rest of the school. For this reason, one orientation measure was calculated which regarded the squid as a line segment rather than as a directed vector and measured the smallest angular deviation between line segments. Such measurements were rarely different from measurements made considering the orientation of the squid and therefore will not be considered further in this paper.

Where measurements of squid length are given, they are of dorsal mantle length from tip of the pen to the tip of the tail. The total length of the squid (including arms but excluding tentacles) is about 1.3-1.5 times the dorsal mantle length (Fields 1965).

RESULTS

Response to Disturbance

One set of factors that caused changes in schooling can be grouped under "external disturbances." These included introducing objects (such as a net) into the water near the squid or tapping on the side of the tank. The typical response was for the squid to group more tightly and, in cases where it was not already marked, to increase the degree of parallel orientation. The amount of change in schooling behavior and the temporal characteristics of this change depended upon the nature and intensity of the disturbance and upon its duration.

One attempt at quantifying the stimulus involved placing an aquarium air stone in the tank. Pressurized air delivered to this air stone in differing amounts and duration produced a stream of bubbles which could be used as a disturbance stimulus of varied intensity and duration. A small stream of bubbles produced little squid reaction, while vigorous water action due to the bubble stream produced marked changes in behavior. Figure 1 shows the changes in three of the schooling indices in response to a moderate disturbance caused by turning on the air bubble stimulus. The degree of parallel orientation, which was already pronounced, did not change appreciably. But the squid did draw noticeably closer together.

Schooling Structure as a Function of Squid Size

Six squid of nearly equal size were haphazardly taken from the holding tank and placed in the experimental tank. The squid swam in this tank for an hour before measurements were made. With the exception of one experiment, a picture was taken of the squid every minute for approximately 1 h. During this other experiment, a picture was taken every 10 s for 10 min. This set of experiments was conducted during the daylight hours of two different days. All of the squid used in this set of experiments had been captured on the same night.

There was a decrease in the mean angular deviation as the size of the squid increased (Table 1). Since small values of the mean angular deviation index are associated with increased parallel orientation, the degree of parallel orientation is greatest in schools composed of large individuals. Even in the case of the small individuals, however, the value of the index does not approach what would be expected if the squid were each orienting in a random direction. In a simulation of 1 million values for six randomly oriented fish, Hunter (1966) found that the mode of the frequency distribution was 69°.

Although the average values for mean angular deviation do give a measure of average departure from parallel orientation for a whole experiment, they do not give an indication of how variable a particular group of squid is in its orientation over time. For example, an experiment of 30 pictures and an average value of the mean angular deviation index of 20° could have had all of the 30 values close to 20°. This would indicate a consistent moderate degree of parallel orientation over time. On the other hand, such an average value could also come from a situation where the squid had strong parallel orientation part of the time and were much more loosely oriented the rest of the time (e.g., the index value could have been 10° on 15 frames and 30° on 15). This kind of difference can be detected if a measure of the variability of the mean angular deviation index for each experiment is calculated. The variability (standard deviation, SD, Table 1) increased with decreasing squid size, indicating that not only do the smaller squid not orient on the average in as parallel a manner as larger squid, but they are also more temporally variable in their orientation. This difference can also be seen if individual experiments are examined. Figure 2 shows the values for mean separation distance and mean angular deviation

TABLE 1.—Relationship between average size of *Loligo opalescens* and parallel orientation and separation of individuals in the six-squid experiments. Each index was calculated for each frame.

Group number	Mean mantle length (cm)	No. frames examined	Mean angular deviation index (degrees)		Mean separation distance index (cm)	
			$\bar{x}$	SD	$\bar{x}$	SD
1	7.5	44	32.0	18.4	32.3	26.5
2	7.6	58	29.0	15.3	25.6	8.0
3	7.7	60	18.1	10.7	16.2	4.5
4	9.7	19	18.5	5.7	14.0	4.2
5	9.7	62	16.2	6.2	18.7	5.2
6	10.2	69	17.2	6.6	20.9	5.0
7	11.9	65	11.1	5.6	18.5	4.0
8	12.0	55	9.6	2.8	15.3	2.7
9	12.0	46	9.1	4.2	13.8	3.0

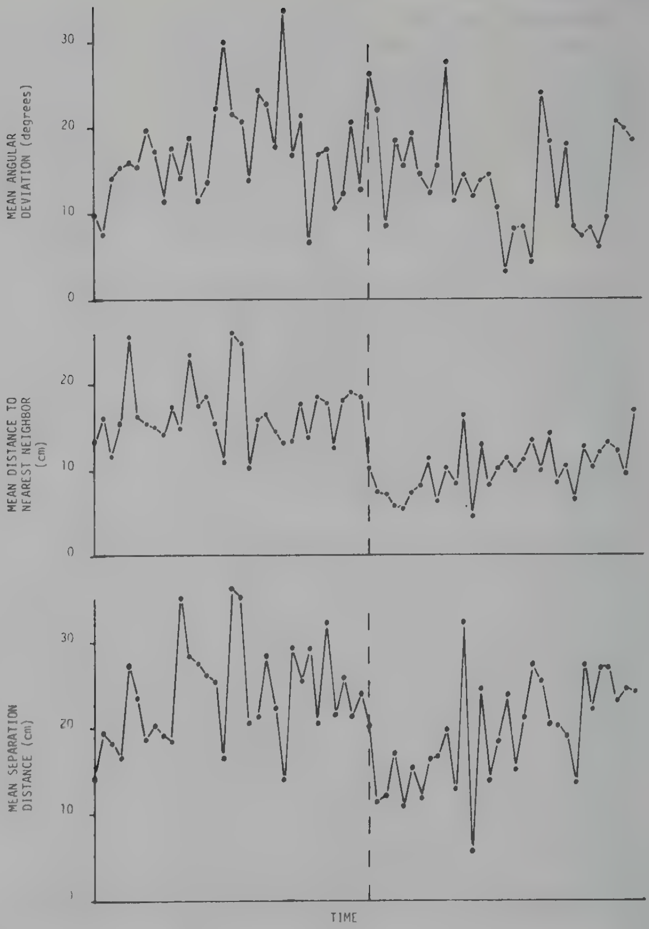

FIGURE 1.—Values of schooling indices for a school of six *Loligo opalescens* before and after disturbance (turning on bubbler). Dashed line indicates when air was turned on. Pictures were taken every minute for 64 min.

for two (Groups 3 and 7) of the experimental runs summarized in Table 1. The parallel orientation is stronger and the variability less in the larger squid (Figure 2C, D). The mean separation distance index is not as clear a function of size (Table 1; Figure 2A, B).

Schools in the Ocean

Very little is known of the natural behavior of *Loligo opalescens* when it is not in large mating schools. In many areas, there often is a large concentration of squid in the vicinity of the deep-scattering layer (C. Recksiek, Moss Landing Marine Laboratories, Moss Landing, CA 95039, pers. commun., October 1976) and large layered concentrations of *L. opalescens* have been reported by those involved in submersible exploration (A. Flechsig, Sea Grant Marine Advisory Service, University of California at San Diego, La Jolla, CA 92093, 1973). There is evidence to indicate, however, that *L. opalescens* is often found in much smaller schools and that these schools contain a narrow size range of individuals. Fields (1965) presents data on the uniformity of size of young squid taken from the same fish catch (presumably the same squid school) and speculates that the size ranges in the schools he observed represent approximately one-half or less than one-half of a year's growth.

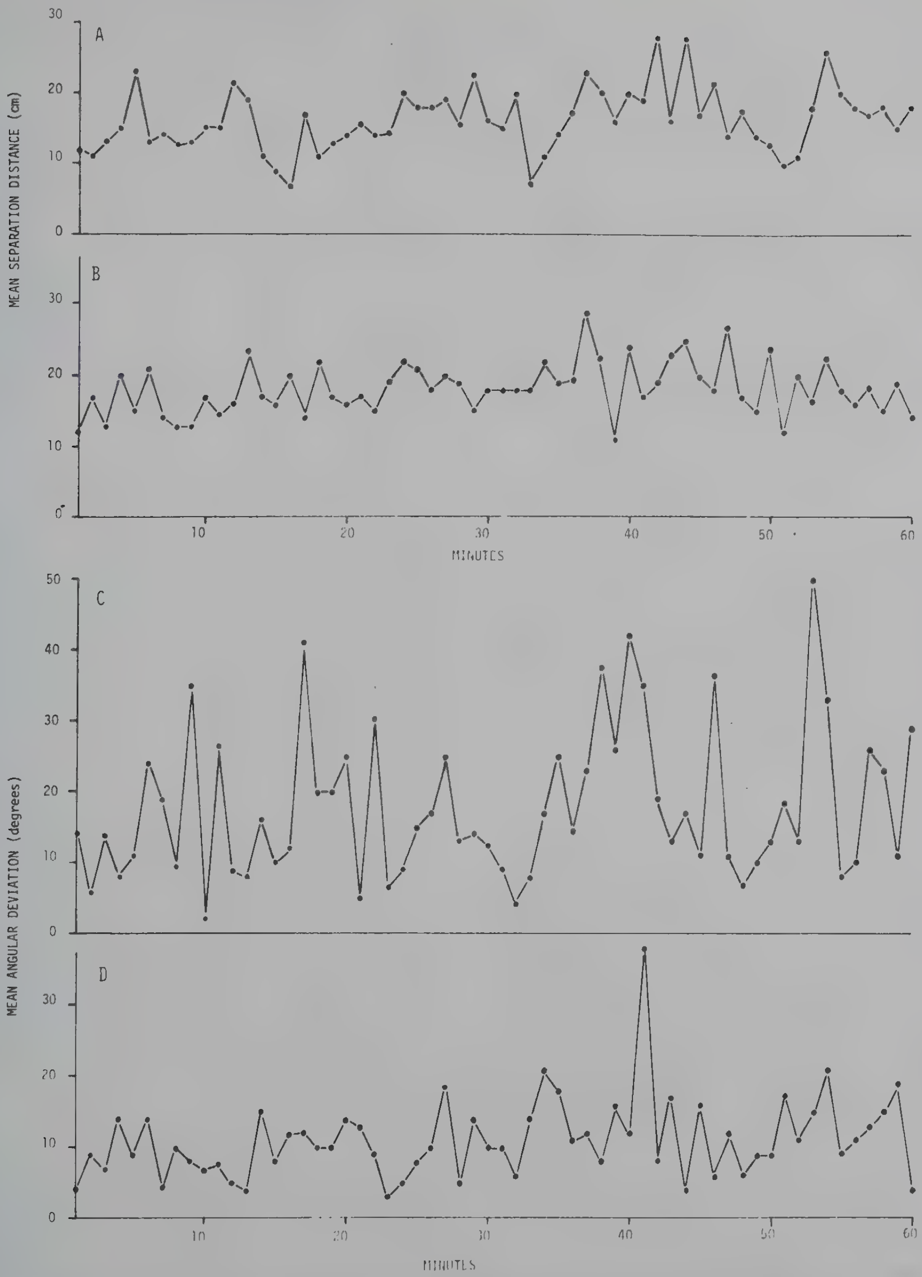

FIGURE 2.—Values of mean separation distance and mean angular deviation for two (Groups 3 and 7) of the experiments presented in Table 1. Mean size of *Loligo opalescens* in the experiment represented in A and C was 7.7 cm mantle length. Mean size of squid in the experiment represented in B and D was 11.9 cm mantle length.

I also obtained data on the uniformity of size in individuals of the same school. The squid were caught during a 1-wk period in August in locations ranging from San Diego to Santa Catalina Island, Calif. A night-light was placed off the stern of the ship in the center of an L-shaped 3-m long mesh net. Squid were attracted to the light and would rush into the net. The net was then raised and the squid could be removed with dip nets. The "schools" were all of the squid which swam into the net at the same time. Squid caught during this period ranged from 5.8 to 17.3 cm dorsal mantle length. But for a given school, they were much more uniform in length. The average size range for 29 schools of 2 to 32 individuals was 2.5 cm.

Maintenance of School Structure and Orientation

Experiments in the laboratory have indicated that vision is sufficient sensory input to mediate schooling behavior. Squid on different sides of a clear, rigid Plexiglas barrier will readily school with each other and they appear to maintain the same type of parallel orientation that is present in normal schooling behavior. Preliminary experiments using such Plexiglas barriers were run to try to elucidate the mechanisms by which spacing is maintained.

Two-Squid Experiments

Experiments were run to determine whether squid would school in the same manner with or without a clear Plexiglas barrier in place. Measurements were obtained for squid swimming together and for the same squid swimming on opposite sides of a Plexiglas barrier which divided the tank into two compartments. The order of the treatment was randomized for each pair of squid. Squid ranged in size from 7 to 13 cm mantle length. For a given experiment, the two squid were of similar length. Pictures were taken of the squid in each treatment every 10 s for 3 min after they first came together and again every 10 s for 3 min after the squid had been left undisturbed for 15 min. If the squid did not come together to within at least 0.5 m within 1 min, the experiment was terminated.

Table 2 shows the results of five such experiments. The first 3-min periods have been compared with each other, as have the later runs. This was to see if the pattern of schooling changed after the squid became more adapted to the experimental regime. This table presents results for the median nearest distance between the two squid for each run and for the median separation angle for these same runs. Separation angle for each frame is simply a measurement of the angle between the two squid and is a measure of orientation (0° separation angle indicating parallel alignment facing the same direction).

TABLE 2.—Median nearest distances and median separation angles for two-squid (*Loligo opalescens*) experiments.

Item	With barrier	Without barrier	Difference[1]
Nearest distance (cm) first 3 min	20.6	16.2	$P<0.05$ barrier greater
	11.3	6.6	$P<0.01$ barrier greater
	38.6	11.65	$P<0.01$ barrier greater
	14.9	7.9	$P<0.01$ barrier greater
	13.8	6.4	$P<0.01$ barrier greater
Nearest distance (cm) second 3 min	24.2	15.8	$P<0.01$ barrier greater
	18.4	6.3	$P<0.01$ barrier greater
	23.9	18.35	$P<0.05$ barrier greater
	14.35	13.1	$P<0.05$ barrier greater
	12.5	8.2	$P<0.01$ barrier greater
Separation angles (degrees) first 3 min	16.4	52.7	$P<0.01$ barrier less
	24.3	11.2	$P<0.05$ barrier greater
	75.1	21.0	$P<0.01$ barrier greater
	21.2	12.2	NS[2]
	17.0	30.9	$P<0.05$ barrier less
Separation angles (degrees) second 3 min	28.2	15.4	$P<0.05$ barrier greater
	15.4	13.6	NS
	19.1	18.0	NS
	25.4	18.3	NS
	11.1	24.9	$P<0.05$ barrier less

[1] Significance of difference in medians from Mann-Whitney *U*-test.
[2] NS = no significant difference, $P>0.05$.

The barrier has an effect upon the separation distance between the two squid. In all cases, there was a significant difference between the distance between squid with and without the barrier. When the Plexiglas barrier was present, the squid tended to space themselves farther apart. There is not a clear relationship between angular separation and the presence of the barrier. Of the six runs showing significant differences, three had greater median separation angles with the barrier in place and three had greater median separation angles when the barrier was not present.

Three-Squid Experiments

The experimental tank was divided crosswise into three equal compartments (1 × 2 m each) by clear Plexiglas partitions. A squid was chosen from the holding tank and was placed in the central compartment. Then a squid for each of the outer compartments was selected. These squid were assigned at random to each of the outer compartments. The squid were allowed to adapt to the experimental situation for 15 min and then were filmed for 5 min (one picture every 10 s). The two outer squid were then switched from one outer compartment to the other and the squid were again allowed to adapt for 15 min. They were then filmed for 5 min (once every 10 s). Squid in these experiments ranged from 9.2 to 15.3 cm mantle length.

It was hoped that this experimental design would indicate whether the center squid, if given a choice, would choose to school with a larger or smaller squid or one closer to its own size. One way to determine whether such a choice is being made would be to determine whether the center squid spends more of its time closer to one outer squid than to the other. Each 5-min run was considered as a unit and each frame was scored according to which outer squid the center squid was nearest. For each run, the data were compared with a binomial distribution which assumed that the center squid had an equal probability of being closest to either outer squid. Of the 17 runs, 16 showed a significant deviation from the expected binomial distribution ($P \leq 0.05$ for 1; $P \leq 0.01$ for 15). These 16 runs were now grouped according to whether the center squid was closest to the larger or smaller outer squid. In 8 of the 16 cases, the center squid was nearest the larger outer squid, while in the other 8 cases, it was nearest the smaller squid. There is no evident preference for large versus small squid. The data can also be arranged to determine whether the center squid spent most of its time near the squid closer to its own size. There were 14 runs for which it was possible to say that the center squid was closer in size to one of the outer squid. Of these 14 runs, the center squid was significantly nearer to the squid closer to its own size 9 times and nearer to the squid farther from its own size 5 times.

These experiments may be viewed in another way by looking at the absolute position of the squid in the tank. The nearest distances of the squid to the Plexiglas barriers were calculated for each frame. These data are summarized in Figure 3 for the 17 runs. The side squid usually are very near the barrier which separates them from the center compartment, while the center squid varies his position within the center compartment, but approaches the Plexiglas barriers much less often.

DISCUSSION

Pelagic fish and squid represent a striking case of convergent evolution, not only morphologically (Packard 1972), but behaviorally as well. One aspect of behavior where this is particularly apparent is schooling. Since many of the same ecological pressures exist for both pelagic groups, it is not surprising that some sort of schooling behavior would have developed in both fish and squid. What is surprising, given the very different physiology and mode of locomotion, is that so many aspects of this behavior are the same.

Loligo opalescens fits Breder's (1967) definition of obligate schoolers. Single *L. opalescens* are rarely caught in the field, and they immediately come together when placed in a tank in the laboratory. As has been reported for many species of fish (Radakov 1973), *L. opalescens* schools consist of individuals of approximately the same size. It has been suggested that the reason that fish school in such groups has to do with swimming speed. Small and large individuals would not swim at the same speed and thus would not normally stay together. This is possibly also true for squid, but data on the swimming speed of large and small *L. opalescens* are not available to substantiate the argument. For several reasons, the swimming speed hypothesis seems less plausible for squid than for fish. In schools of fish which show parallel orientation, the fish continually maintain forward motion and thus swimming speed is likely to be an important factor. But field and laboratory observations have indicated that individuals in squid schools spend much of their time hovering in the same position in the water column with only

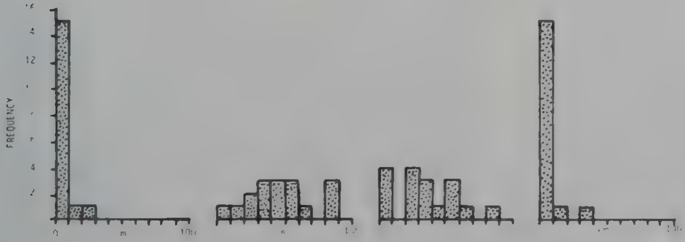

FIGURE 3.—Histograms of mean nearest distance between *Loligo opalescens* and barrier in the 17 three-squid experiments. Distances are broken up into 10-cm intervals. From left to right: left outer squid to left barrier, center squid to left barrier, center squid to right barrier, right outer squid to right barrier.

slight backward and forward motion caused by jets of water from the siphon. Even when disturbed, the squid do not make long extended swims which would tend to sort out those of differing swimming ability. In the field, the most common response of a squid school to a disturbance (the presence of a scuba diver or a shark) is to clump closer together and move off a slight distance. On one occasion when I was diving in a large spawning school (several thousand individuals), the squid executed the same type of maneuver that has been reported for fish schools. Instead of moving off, the school completely enclosed me, leaving a spherical space of approximately 3 m radius around the "predator."

One other piece of evidence suggests that it is not differences in swimming speed alone which cause the squid to school according to size. While diving in the Bahamas in the Hydrolab underwater habitat, we observed a school of squid which routinely visited the habitat. This school was composed of *Doryteuthis plei*, a species which quite closely resembles *L. opalescens* and presumably has similar swimming ability. This school consisted of seven squid and, in this case, was not composed of individuals of the same size, the largest individual being at least two times the length of the smallest individual. We chased this school several times but were never able to force them to separate. The smallest squid maintained the same swimming speed as the largest squid.

It is possible that squid maintain schools of individuals of a fairly narrow size range because of social factors. Generally, workers studying schooling have assumed that all of the fish in a school may be treated as equivalent individuals in the production of the behavior and that there is no social structure in the schools. In fact, some workers have suggested that schooling is really just a modified form of individual cover-seeking behavior (Williams 1964; Hamilton 1971). This assumption of equality of individuals may be an untenable one for squid schools. In the field, Hochberg and Couch (1971) observed signaling by some members of a school of *Sepioteuthis sepioidea* which they felt prevented other squid from joining the school. Furthermore, in the laboratory, I have observed complicated agressive interactions in *L. opalescens* which certainly demonstrate that all squid cannot be considered behaviorally equivalent individuals at all times (Hurley 1977).

One aspect of schooling in fish which has been emphasized by many workers is that the structure of schools may change as a function of the age or the physiological condition of the fish. Van Olst and Hunter (1970), for instance, found that in five species of marine fishes, schools of young fish were less compact and showed greater differences in angular headings than did schools of adult fish. In addition, Hunter (1966) showed that distances between jack mackerel tended to increase with food deprivation, while Keenleyside (1955) noticed that sticklebacks were more densely packed in a school when well fed than when starved.

I attempted to determine whether similar phenomena were observable in squid schools. Schools of small squid (7-9 cm mantle length) gave the impression of being less cohesive than schools of larger squid (13-15 cm mantle length). This was supported to some extent by the quantitative measurements, particularly those of angular orientation. The variability was also higher for all of the indices for the smaller squid. It has been suggested for fish (Van Olst and Hunter 1970) that the observed change with size could have been an adaptation to the higher food requirements of the juvenile fish. This speculation is supported by observations that a number of species school less cohesively under conditions of food deprivation. The same explanation may also hold for squid, but my existing data do not support it. I ran two experiments in which schools of six squid were filmed before and after feeding. In one experiment, there were no significant differences in the schooling indices before and after feeding, while in the other, there was significantly less school cohesion and parallel orientation after feeding. In any event, it is not possible to guess which factors are instrumental in this increased cohesiveness and consistent geometry.

As is the case for fish, vision seems to be the primary sensory system used in squid schooling. Squid will readily school across a clear, rigid Plexiglas barrier, although they tend to stay somewhat farther apart than they normally would. Investigators dealing with fish also found that the presence of a clear, rigid barrier caused abnormalities in the spacing between individuals, in some cases increasing the fish-to-fish distance (Cahn 1972) and in some cases decreasing it (Shaw 1969). These workers speculated that this change was due to lack of lateral line input and a resultant loss of information concerning the position of the adjacent fish. Squid do not have a similar extensive vibration-sensitive system, although they may be able to detect vibrations with their statocysts. In the case of *L. opalescens*, the most likely explanation for this change in spacing is that the presence of the barrier physically limits the extent to which each squid can compensate for the other individual's movements. In the experimental tank, squid seemed to differ in their motivation to school. When the barrier was not present, a squid with a strong tendency to school could always maintain proximity to another squid. But if the barrier were present, that squid could only follow another squid as far as the barrier and had to remain there until the other squid returned.

I had hoped that the experiments with the three squid separated by Plexiglas barriers would give some clue as to whether the squid actively chose to school with individuals of the same size, but the results were inconclusive. The results did indicate, however, a possible mechanism for maintenance of spacing within a school. The center squid tended to stay toward the middle of the compartment, while the side squid maintained positions very near the Plexiglas barrier. It is possible that the center squid was attempting to equalize the visual angle subtended by the squid on each side, while the outer squid were attempting to get into positions with squid on each side. The measurements of visual angle which I can get from my photographs are not accurate enough to determine whether this is happening. If outer squid are continually trying to achieve a position where they have squid on either side of them, individuals in a school should be continually shifting positions. Casual observations have indicated that this does happen some of the time; but at other times, the individuals maintain the same positions relative to one another.

An area where a comparison of squid and fish schooling may be useful is in the speculation concerning the evolution of the schooling behavior and its possible advantages. Many recent papers have concentrated on the hydrodynamic advantages of fish schooling (e.g., Breder 1976) and base their explanations of many of the details of school structure on the fish mode of tail-flip locomotion and the vortices which are subsequently created. Van Olst and Hunter (1970) suggest that the typical nearest neighbor distance in fish schools is about one-half a body length and that this distance may be explained by considering the amplitude of the tail beat in swimming. It is interesting that in squid, with their very different mode of locomotion (jet propulsion as opposed to tail flips), the spacing between nearest neighbors is still maintained between one-half and one body length in undisturbed squid.

Other investigators have speculated that a primary function of schooling is as a defense against predation. (See reviews by Shaw 1970 and Radakov 1973.) Squid have many of the same reactions to disturbance that fish do. They both clump more closely together as a result of disturbance and both have been seen to surround their predators. Further evidence which suggests that predator defense may be an important function of squid schooling comes from the development of the behavior in juvenile squid. In the course of rearing *L. opalescens* (Hurley 1976), I made observations on schooling behavior. The newly hatched squid appeared to have no attraction to each other, but after 6 or 7 wk schooling was occasionally observed. This schooling was only evident in response to disturbance (tapping on the tank or putting a net into the water). When the squid were feeding undisturbed, there was no obvious schooling behavior.

ACKNOWLEDGMENTS

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7818

III. BIOENERGETIC SPECTRA OF SKIPJACK AND YELLOWFIN TUNAS

James F. Kitchell

William H. Neill

Andrew E. Dizon

John J. Magnuson

A. *Introduction*

A major research facility devoted to the study of captive tunas (Nakamura, 1972) has provided some opportunity to develop greater understanding of the biology of the skipjack tuna *(Katsuwonus pelamis)*. Evidence to date indicates remarkable adaptation to pelagic environments and an unusual physiology associated with life in relatively warm but unproductive waters (Brock, 1974; Magnuson and Heitz, 1971; Magnuson, 1973; Stevens and Neill, in press). Remarkable features of skipjack tuna biology include (a) obligatory continuous swimming associated with the absence of a gas bladder (Magnuson, 1973) and lack of respiratory pumps (Brown and Muir, 1970); (b) warm-bodiedness owing to retention of metabolic heat via countercurrent heat exchangers in the blood-vascular system (Stevens and Fry, 1971; Stevens, Lam, and Kendall, 1974; Neill, Chang, and Dizon, 1976); and (c) activity-dependent respiration rates that appear independent of both ambient temperature (Gordon, 1968) and the allometric effect of weight (Gooding and Neill, ms).

All the tunas are extremely difficult to maintain for experimental work. Because animals often die shortly after handling (e.g., following weight determination), studies are limited in scope and duration. Nonetheless, recent and ongoing work (Neill *et al.*, 1976; Sharp and Francis, 1976; Kitchell, Magnuson, and Neill, 1977; Gooding and Neill, ms; Uchiyama and Strusaker, ms; Barkley, Neill and Gooding, ms) has provided data and concepts that permit establishment of a hypothetical yet holistic framework for future research on tuna bioenergetics.

In this paper, we attempt to combine principles of bioenergetics with data from experimental and field studies to construct energy budgets for skipjack tuna and thereby define this scombrid's scope for growth (Warren, 1971). Using data of Sharp and Francis (1976), the analysis is then extended to yellowfin tuna *(Thunnus albacares)*. Our goal in this effort has been a more coherent characterization of the growth process

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in tunas and identification of those physiological, behavioral, and/or ecological processes that have the greatest potential for improved understanding of tuna biology.

B. *Energy Budget Components and Their Units*

Using conventional symbol notation (Ricker, 1971), the mass balance or energy budget equation may be written

$$C = R + U + F + G + \Delta B \qquad (1)$$

where

C = rate of food consumption

R = rate of metabolism (respiration)

U = rate of excretion

F = rate of egestion

G = rate of gamete production

ΔB = rate of growth

Our handling of budget terms has necessitated subdivision of R into two component parts:

$$R = SDA + M ,$$

where SDA (specific dynamic action) is the rate of energy cost associated with processing the input energy sourse (mainly, deamination of proteins) and M is the rate of energy expenditure associated with the remainder of metabolic work, or net metabolism (basal metabolism and activity).

Each term in the equation may be defined in biomass equivalents in developing mass-balance solutions. Because the calorie functions as the common denominator in bioenergetics (Warren, 1971), the equation may also be written in caloric units if energy equivalents are known for biomass units and catabolic processes.

To facilitate calculations, all parameter estimates are given in per day units based on a sexually immature 1 kg (live weight) skipjack tuna at 24°C. Caloric values for skipjack biomass are 1.46 kcal/g live weight (Kitchell *et al.*, 1977). Although food habits of skipjack are highly variable (Yuen, 1959; Manar, 1966; Magnuson and Heitz, 1971), volumetric composition approximates 50% invertebrates and 50% fishes; we estimate these to have caloric equivalents of 1.0 kcal/g wet weight and 1/2 kcal/g wet weight, respectively. Thus, mean caloric value of skipjack forage is taken as 1.1 kcal/g wet weight.

C. Energy Budgets for Skipjack Tuna at Six Input-Output Regimes

In this section, we attempt to evaluate the energetics spectrum of skipjack tuna by determining energy budgets at six levels--starvation, maintenance (no weight change), observed growth at three levels of metabolism, and estimated maximum daily ration.

1. Starvation. Lacking any input, energy loss results from (a) metabolic demand; and (b) secretions and excretions. Gooding (Southwest Fisheries Center, National Marine Fisheries Service, Honolulu, personal communication) measured routine oxygen consumption at 24°C for fasted skipjack tuna weighing 0.63 to 3.90 kg. The resulting regression equation was $Y = -0.340 + 0.016X$ ($n = 40$), where $Y = \log_{10}$ mg O_2 consumed per g fish per hour and $X = \log_{10}$ (weight of skipjack, g). Both the basal rate and the weight exponent are substantially greater than those reported for most fish species (Gordon, 1968; Beamish and Dickie, 1967). Using an oxycalorific equivalent of 3.4 cal mg O_2^{-1} (Warren, 1971), routine daily metabolic output of a fasted 1 kg skipjack tuna would be 510 mg $O_2 h^{-1} \times 3.4$ cal $mg^{-1} \times 24$ h $day^{-1} = 42$ kcal day^{-1}. Brett (1971) and Warren (1971) estimate that O_2 consumption measures only 80% of total energy loss associated with mobilizing body tissues for metabolic activity. The remaining 20% is lost both as heat associated with deamination of protein and excreted nitrogenous waste. The former is termed specific dynamic action (SDA) and accounts for approximately 15% of the total output, while the latter is largely ammonia and/or urea containing about 5% of initial energy content. Accordingly, total energy output would be the sum of SDA and calories excreted as metabolic waste products. Empirically, $42/0.8 = 53$ kcal of total energy output $fish^{-1}$ day^{-1}. The energy content of the whole fish is 1,460 kcal; therefore, the rate of loss would be $53/1{,}460 = 36$ cal $kcal^{-1}$ or about 3.6% of total energy content per day (Table I). For a skipjack swimming at or near its minimum speed (V_{100} of Magnuson, 1973), the weight-specific equation for routine metabolism in caloric units becomes $M = 29W^{0.016}$ where M = cal $kcal^{-1}$ day^{-1} and W = fish weight in kilograms.

Because fish utilize high-energy tissues (e.g., fat) and hydrate when starved, weight loss alone is an underestimate of net change in energy (Brett, 1973; Niimi and Beamish, 1974; Kitchell *et al.*, 1977). Skipjack lost about 1.8% of body weight per day (Dizon, Southwest Fisheries Center, Honolulu, personal communication) during the first 25 days of a starvation period. Data from Kitchell *et al.* (1977) indicate change in energy content per unit weight of about 1.8% per day

TABLE I. Estimated Energy Budget Terms at Six Bioenergetic Regimes for a 1 kg Skipjack Tuna at 24°C [a]

Bioenergetic regime	Requisite ration	Process rate (cal $kcal^{-1}$ day^{-1})					
	(% body wt. day^{-1})	Consumption (C)	Net Metabolism (M)	SDA	Excretion (U)	Egestion (F)	Growth (ΔB)
Starvation	0	0	29	5	2	0	-36
Maintenance	5.9	44	29	7	2	7	0
Observed growth at							
1 Lab M (= Level I)	7.3	57	29	9	3	9	7
2 Lab M (= Level II)	13.1	99	58	15	5	15	7
3 Lab M (= Level III)	19.0	143	87	21	7	21	7
Maximum	30.0	250	87-155	38	12	38	7-69

[a] *Daily ration is given as percentage of body weight consumed per day assuming 1.1 kcal per gram live food.*

for skipjack starved 10 days. Combining absolute weight changes with changes in caloric density yields an independent estimate of 1.8 + 1.8 = 3.6% loss per day, exactly the value determined from the balanced energy budget.

2. *Maintenance.* Calculation of a maintenance ration must include outputs proportional to feeding level as well as routine metabolic rate. Although experimental data which would provide measures of rates of excretion, egestion, and SDA for skipjack tuna are not available, we can estimate these rates based on studies with other fishes.

Excreted energy includes by-products and wastes, such as ammonia and urea, resulting from deamination of consumed protein. Caloric output is generally taken as 3% to 7% of consumed calories (Winberg, 1960; Mann, 1967). Using a mean of 5%, we estimate excreted energy, U, as a constant proportion of consumption rate, C; thus, $U = 0.05C$.

Egestion or fecal output can be similarly estimated as a constant proportion of consumption; exacting studies of carnivorous fishes indicate that absorption efficiencies are not strongly related to feeding level (McComish, 1970; Kelso, 1972). Of the calories consumed as invertebrate foods we estimate that 20% would be egested (McComish, 1970), whereas as little as 10% of calories consumed as fish would be egested (Kelso, 1972). Using a mean of egested calories, we estimated $F = 0.15C$ for the mean diet.

As described above, the specific dynamic action component of energy output, SDA, is broadly defined as the energetic cost of converting food for catabolic and/or anabolic processes

(Warren, 1971). Based on the experimental data of Muir and Niimi (1972) and Beamish (1974), we estimate that 15% of consumed calories are expended as heat in SDA; thus, SDA is set equal to 0.15C.

Using the measured value of routine metabolism for a fasted fish, substitution in equation 1 yields

$$C = (42 + 0.15\ C) + 0.05\ C + 0.15\ C + 0 + 0\ ;$$

therefore,

$$0.65\ C = 42\ ; \tag{2}$$

$$C = 65\ \text{kcal fish}^{-1}\ \text{day}^{-1}\ ;$$

and,

$$C/1{,}460 = 44\ \text{cal kcal}^{-1}\ \text{day}^{-1}\ .$$

In biomass units, a 1 kg fish must consume 65/1.1 (assuming a mixed diet) = 59 grams of food for a maintenance ration of 5.9% of fish weight per day (Table I). This estimate of maintenance is derived for fish swimming at or near their minimum speed in a respirometer, and should not be construed as representative of the minimum energy requirements of fish in nature. Note, however, that the maintenace ration for skipjack tuna is equivalent to or greater than the maximum ration for most nonscombrid fishes of equivalent size (Magnuson, 1969).

3. Observed Growth at Three Levels of Activity. Mann (1967) described the assumptions of what we call the Winberg approach (Winberg, 1960), which has been widely applied in fish energetics studies (see Backiel, 1971; Healy, 1972; Burbridge, 1974; Ware, 1975). Briefly restated, the routine metabolic rate determined in a respirometer is doubled to estimate metabolic levels for most fishes under natural conditions. More recently, Ware (1975) estimates that a threefold increase might be more appropriate for applications to pelagic fishes. Bioenergetic studies of terrestrial vertebrates employ a similar 2-3x multiplier for field applications (Brody, 1945; Dutton, Fitzpatrick, and Hughes, 1975).

To estimate an energy budget for normally growing, minimally active (Level I) skipjack tuna, we combined parameters of a maintenance budget with an observed growth rate of 0.7% in weight per day for 1 kg skipjack as calculated from growth curves (Uchiyama and Struhsaker, ms) and length-weight relations (Magnuson, 1973). Growth is equivalent to $0.007 \times 1{,}460\ \text{kcal} = 10\ \text{kcal fish}^{-1}\ \text{day}^{-1}$; thus the budget equation is

$$0.65\ C = 42 + 10$$

or $$C = 80\ \text{kcal fish}^{-1}\ \text{day}^{-1}\ .$$

The daily ration would be 80/1.1 = 73 gram food per 1 kg fish or about 7.3% per day for 0.7% day^{-1} growth in weight or a gross growth efficiency of about 10% (Table I).

By assuming that higher levels of activity in nature result in a twofold increase in routine metabolic rate (Level II), the equation becomes

$$0.65\ C = 2(42) + 10$$

or $$C = 145\ \text{kcal fish}^{-1}\ \text{day}^{-1}\ ,$$

which converts to a ration of 13.1% per day. Assuming a threefold increase in routine metabolism (Level III) yields C = 209 kcal per fish or a daily ration of approximately 19.0% (Table I) Gross growth efficiencies would be 5% and about 4%, respectively for the higher activity levels.

4. *Maximum Input-Output of Energy*. To evaluate this energy budget we set the input parameter, C, to its maximum, calculated outputs, and compared the results with those determined independently from observation or experimentation. When combined with known metabolic rates or maintenance rations, the scope for growth is delineated as defined by Warren (1971).

Digestion rate and relative stomach volume intrinsically limit rates of food consumption. Within a species both are inversely related to fish size. As a result the maximum daily ration, C_{max}, declines allometrically with weight, W, and may be written as $C_{max} = aW^{-b}$.

Based on previous *ad libitum* feeding studies using whole fish as food (Magnuson, 1969), the maximum daily ration of a 1.5 kg skipjack was estimated as 15-20%. Recent studies by Steffel (Southwest Fisheries Center, Honolulu, personal communication) indicate that smaller food particles are more readily consumed and that maximum rations for 1.4 kg skipjack are approximately 28-35%. Using a value of 30% and converting to caloric units assuming natural foods, estimated consumption would be 330 kcal total or about 225 cal kcal^{-1} biomass day^{-1}. The value of the weight exponent, b, is not available for skipjack but may be estimated as -0.3 based on results for other fishes (Brett, 1971; Niimi and Beamish, 1974; Kitchell *et al.*, 1974). Taking b as -0.3 and then estimating a from Steffel's data yields an estimated C_{max} of 250 cal kcal^{-1} day^{-1} for 1 kg skipjack ($C_{max} = 250\ W^{-0.3}$, where fish weight, W, is in kg).

Energy outputs as specific dynamic action (SDA), excretion (U), and egestion (F) are constant proportions of consumption representing a loss of 35% of calories consumed. Thus, energy available for net metabolism, growth, and (in larger fish) gamete production would be 0.65 C_{max}. Limits described by these equations are given as a function of fish weight (Fig. 1).

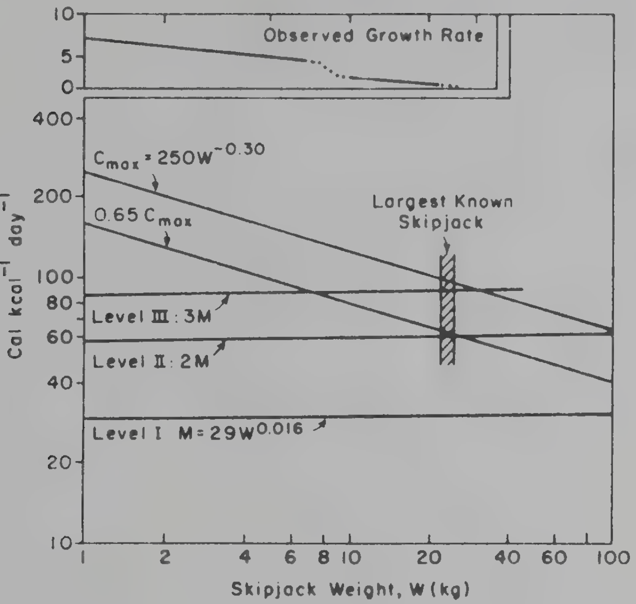

FIG. 1. Relationship of estimated maximum caloric intake and outputs to size of skipjack tuna, Katsuwonus pelamis. *Parameters and symbols are described in text.*

Based on otolith analysis (Uchiyama and Struhsaker, ms), the daily growth increment of skipjack tuna appears to be a nearly linear function of log (weight). Skipjack growth includes energy stored in both somatic growth (ΔB) and gonadal development (G). Subtracting observed growth from 0.65 C_{max} gives an estimate of the energy available for net metabolism. Also plotted in Fig. 1 are the presumed lower (Level I) and upper (Level III) limits of net metabolism as multiples of routine metabolism determined by Gooding and Neill (ms) from captive fish.

Interpretation of Fig. 1 should be made with caution. First, weight-related rate functions are extrapolated from data gathered for small (0.6-4.0 kg) skipjack. Second, no basic physiological or ecological criteria truly justify expressing metabolic rates as multiples of the routine rate. This practice simply serves to characterize relative levels of activity estimated to occur under natural conditions.

D. *Limits on Growth and Maximum Size of Skipjack Tuna*

Differences between rates of maximum energy intake and estimated energy costs (Fig. 1) allow an estimate of bioenergetic limits on growth rate. For example, a 1 kg skipjack feeding at the maximum rate and maintaining a metabolic rate approaching Level III would process $0.65 \times 250 = 162$ cal $kcal^{-1}$ day^{-1} of which $3 \times 29 = 87$ cal $kcal^{-1}$ day^{-1} would be metabolized, leaving 25 cal $kcal^{-1}$ day^{-1} for growth. The observed growth rate is approximately 7 cal $kcal^{-1}$ day^{-1}. If wild skipjack do maintain Level III metabolism, individuals smaller than about 7-10 kg are growing at rates substantially less than maximal. As noted by Ware (1975), active metabolic rates are probably not greater than threefold routine rates. Thus, smaller animals appear limited by food availability and/or their efficiency as predators.

Growth of skipjack larger than 7-10 kg appears limited not by the availability of food but by the maximum rates at which available food can be physically consumed and physiologically processed. This limitation becomes increasingly important as the fish grow larger (Fig. 1). Level III metabolism cannot be sustained in skipjack larger than about 8 kg; at about 25 kg, even Level II metabolism requires more energy than can be provided by C_{max}. We propose that maximum size in skipjack tuna reflects the point of balance between the minimum rate of energy expenditure consistent with normal activity and the maximum rate of energy aquisition (C_{max}), the latter governed largely by factors intrinsic rather than extrinsic to the fish.

Under an assumption of model (Fig. 1) validity, it becomes a simple matter to predict maximum skipjack size given the rate of metabolism at maximum size or, conversely, to predict the normal rate of metabolism in a skipjack of maximum size. The second prediction is the appropriate one because we have from independent sources a good estimate of maximum size in skipjack, but no estimates at all of rates of energy expenditure in wild tunas.

The largest skipjack tuna on scientific record weighed 22 kg (Magnuson, 1973); larger (>25 kg) skipjack are rumored to have been caught. According to our model (Fig. 1) the no-growth point for a 22-kg skipjack tuna eating its maximum daily ration occurs at a level of metabolism slightly more than twice the routine rate extrapolated from laboratory data. While this prediction conforms with Winberg's (1960) conclusion that the mean metabolic rate of fish in nature is about twice the routine rate, its accuracy cannot be judged on the basis of existing data.

In typical fishes, maximum size appears limited not by the size of C_{max} but by progressive inability of fishes to consume at the C_{max} rate--the energy cost of obtaining C_{max} becomes greater than the energy return from C_{max} (Weatherly, 1972). One must presume that this is because evolutionarily C_{max} has kept pace with (or a step ahead of) the average rate at which food is available for consumption. Why has this not, apparently, been the case for skipjack tuna? Perhaps because the bioenergetic strategy of skipjack tuna has been tempered by a peculiar consideration of no relevance in the evolution of typical fishes--a thermal "squeeze" in which skipjack larger than some critical size risk overheating their core tissues at all environmental temperatures higher than the minimum temperature for function of superficial tissues. Under this hypothesis (Neill *et al.*, 1976), the habitat available to skipjack tuna becomes progressively reduced as the fish grow larger, with larger fish restricted to the cooler part of the range habitable for smaller fish. Barkley *et al.* (ms) have extended the thermal-squeeze hypothesis to include an additional restriction imposed by low dissolved oxygen; their resulting model of skipjack distribution by size in the eastern and central Pacific seems reasonably consistent with fishery-catch data and with the apparent migration patterns of skipjack.

Under the assumption that normally active skipjack must maintain an average metabolic rate of 3 mg O_2 $g^{-1}hr^{-1}$ in their red muscle, Neill *et al.* (1976) suggest that the thermally tolerable habitat for skipjack vanishes as the fish approach 22 kg. A routinely active skipjack tuna has a red muscle metabolic rate of about 1 mg O_2 $g^{-1}hr^{-1}$ (Neill *et al.*, 1976); thus, their assumption of a 3 mg O_2 $g^{-1}hr^{-1}$ rate for wild fish is equivalent to presumption that the normal wild rate is thrice the rate measured in routinely active captive animals. Trebling of red muscle metabolic rate is equivalent to doubling of whole-body routine rate if, as seems reasonable (Dizon, Brill, and Yuen, this volume), one-half the routine oxygen demand of the whole animal is attributable to red-muscle activity. In this sense, then, the present bioenergetic hypothesis and the thermal-squeeze hypothesis are consistent: they invoke equivalent metabolic rates to account for the observed maximum size of skipjack tuna. The thermal-squeeze hypothesis makes more tenable the unusual role of C_{max} as a limiting factor in growth to maximum size, for skipjack had nothing to gain evolutionarily by increased C_{max} if risk of overheating set limits on energy output at maximum size.

Skipjack energy budgets (Table I) and extrapolations (Fig. 1) were based on the rates calculated for a constant temperature of 24°C. Would a reduction in temperature with fish size, in keeping with the thermal-squeeze hypothesis, substantially alter the bioenergetic spectrum of skipjack? Probably not, because metabolism and activity in skipjack tuna appear virtually independent of environmental temperature (metabolism--Gordon, 1968; activity--Stevens and Fry, 1972; Dizon *et al.*, in press; Chang *et al.*, ms; Dizon, Brill, and Yuen, this volume).

E. *Bioenergetic Limits for Yellowfin Tuna*

Sharp and Francis (1976) estimated energy budget parameters for yellowfin tuna in the eastern Pacific. Beginning with Gooding and Neill's (ms) estimates of metabolic rate in skipjack tuna, they assumed that yellowfin metabolic weight was better approximated as $W^{0.8}$. Thus, the equation for routine metabolism of yellowfin became $M = 29\ W^{-0.2}$, where M is in cal $kcal^{-1}$ fish day^{-1} and W is fish weight in kilograms. Caloric density of yellowfin biomass was assumed to be similar to skipjack (Sharp and Francis, 1976). Consideration of calculated daily ration as a function of yellowfin weight (see Sharp and Francis, 1976: fig. 5) leads us to suppose that C_{max} (in cal $kcal^{-1}$ day^{-1}) = $190\ W^{-0.35}$. Therefore, the maximum rate at which energy is available for growth and net metabolism in the yellowfin is $124\ W^{-0.35}$ cal $kcal^{-1}$ day^{-1} (= $0.65\ C_{max}$).

As for skipjack (Fig. 1), now we can estimate relationships between metabolic levels, maximum available energy, and fish size for yellowfin (Fig. 2). The exercise leads to a conclusion identical to that reached above for skipjack tuna: maximum available energy and the energy required for metabolic

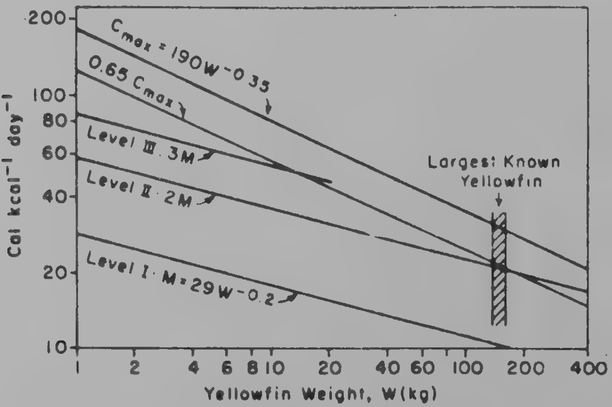

FIG. 2. Relationship of estimated maximum caloric intake and outputs to size of yellowfin tuna, Thunnus albacares. *Parameters and symbols are described in text.*

levels slightly in excess of twice the routine rate converge at a weight equal to approximately that of the largest yellowfin tuna on scientifically valid record--182 kg (Sharp, personal communication).

F. Discussion

Our bioenergetic analysis suggests that small skipjack and yellowfin tunas are growth-limited by food availability but that larger fish are growth-limited by their ability to consume and process available food. For each species, maximum observed body-weight corresponds approximately with that weight at which the maximum daily ration just fails to support a level of energy expenditure about twice that of the fish swimming at its minimum speed for hydrodynamic equilibrium.

Despite the qualitative similarity between species, there remains a striking quantitative difference: yellowfin tuna reach a maximum weight more than eight times that attained by skipjack tuna. Bioenergetically, the difference in maximum weights resolves itself principally as a difference in the weight exponents of metabolic rate. Specific metabolic rate of yellowfin tuna, presumably like that of typical fishes, is assumed to be proportional to $W^{-0.2}$; whereas, metabolic rate of the skipjack seems nearly independent of weight (i.e., $M \propto W^0$. This difference, in turn, may reflect the presence and absence of a gas bladder in yellowfin and skipjack tunas, respectively. A gas bladder seems hydrodynamically obligatory for those tunas obtaining weights greater than 60 kg (Magnuson, 1973). The skipjack is among the largest of scombrids without a gas bladder. Absence of a gas bladder presumably enables skipjack to make vertical movements that are more rapid than those of which the yellowfin is capable. Thus, the skipjack would seem better adapted than yellowfin for exploitation of the epipelagic zone's vertical dimension, at least in terms of such speed-demanding activities as prey pursuit and predator avoidance.

For skipjack tuna, we have accounted for the unusual size-limiting role of maximum daily ration (C_{max}) by suggesting that evolution of increased C_{max} was obviated by another, more inflexible, limit on maximum size--a size-progressive thermal squeeze, comprising convergence of the environmental temperature maximum for necessary dissipation of metabolic core heat with the minimum temperature (perhaps 15°C--see Dizon *et al.*, in press) for function of more peripheral tissues such as skin, gills, eyes, and brain. Can the thermal-squeeze argument also be made for yellowfin tuna? Perhaps so, but with less confidence than for the skipjack. The yellowfin tuna (a) appears capable of substantial physiological thermoregulation on a short-term basis (Dizon, recent unpublished data); and (b) exhibits a marked reduction in swimming speed--and presumably in metabolic rate--with decline in temperature ($Q_{10} \sim 2$--Dizon *et al.*, in press). Therefore, the yellowfin tuna may not be subject to risk of overheating as it grows to maximum size.

It seems paradoxical that food availability should fail to be growth-limiting for large tunas, given that they live in what surely must be one of the most unproductive environments inhabited by fishes--the epipelagic zone of tropical seas. Reid (1962) indicates that broad regions of the central Pacific Ocean contain average net-zooplankton densities on the order of 25 parts per *billion* or less. Adult tunas feed at least one trophic level higher than net-zooplankton; thus, water with 25 ppb net-zooplankton might contain only about 2.5 ppb of tuna forage. That large tunas even survive in such a food-dilute environment--let alone obtain maximum daily rations--must testify both to the high degree of patchiness in distribution of tuna-forage and to a remarkable ability of tunas to locate and harvest aggregations of forage.

In conclusion, we suggest that the energetic limitations of skipjack, yellowfin, and, perhaps, most other tunas vary as a function of body size. Growth rates in small fish appear largely limited by food resources. Reduced growth rates in large fish may, in part, be due to increasing limitations of food-resource availability but more probably are due to the physiological limits imposed by adaptations which make tunas very efficient predators.

Evaluation of our hypotheses can be achieved by directly determining rates of feeding and/or metabolism in wild tunas. Because the former seems least logistically feasible, we recommend the latter. Laboratory studies could be employed to calibrate an ultrasonic telemetry system that monitors body-temperature differentials. If applied in conjunction with high-seas tracking of tunas, such an approach would provide an unique opportunity to determine actual habitat-activity level interactions for a free-swimming fish and, ultimately, the kinds of information that would allow a quantum increase in knowledge of tuna biology.

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REPORTS

Fishing for Anchovies off California

REUBEN LASKER
U.S. Dept. Commerce, NOAA, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California, U.S.A.

The recently adopted Anchovy Fishery Management Plan (Pacific Fishery Management Council [PFMC], 1978) mandated by the Fishery Conservation and Management Act of 1976 which established the 200-mile fishery zone for the United States, provides a formula for setting an annual optimum catch of the northern anchovy, *Engraulis mordax*, by U.S. and foreign fishermen off the California coast. Like the Peruvian anchoveta and the Atlantic menhaden, the northern anchovy is mostly reduced to fish meal and oil and provides an important protein supplement for poultry and other animal feeds.

The last two triennial surveys for fish eggs and larvae (1975 and 1978) by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) provided data from which spawning biomass estimates were made. They showed that there was a significant decline in the total anchovy spawning biomass over the 3-year period, from 3.3 million metric tons to 1.2 million metric tons. Natural variability in the size of the anchovy central stock is well documented and this spawning stock size, 1.2 m tons, was last recorded in 1961 (PFMC, 1978). Information obtained from the fishery showed that the 1974 and 1975 year classes were very poor and contributed to the decline in the whole anchovy population, although the 1976 year class was better than average. Until 1978, fishing on the anchovy was regulated by the Fish and Game Commission of the State of California and was held to a modest take, approximately 163 000 tons in 1975. With the advent of an unregulated Mexican fishery on the same stock south of the border, the 1977 catch totalled approximately 257 000 tons (Mexico, 157 000; U.S., 100 000).

A combination of heavy fishing on the spawning stock with the coincidence of a number of successively poor year classes has depressed other clupeoid stocks (Murphy, 1977). Whether a 257 000 ton fishery can be considered to be 'heavy fishing' is unknown for this stock, but the Anchovy Plan would have restricted this much fishing if the spawning biomass had been known to be low for 1977; no assessment cruise was made in 1977, nor was the plan in effect at that time. So far Mexico has not adopted the U.S. plan, and fishes this stock without restriction. While fishing can be regulated in each country by political means, the causes of natural fluctuations in population size remain largely unknown although the so-called 'stock and recruitment problem' is an active area of research throughout the world.

Briefly stated, the following questions are asked: 'What are the major factors controlling reproduction and larval survival, and what is the impact of reduced stock size on the strength of future recruitment into a year class?'

Studies at the Southwest Fisheries Center of NOAA (National Oceanic and Atmospheric Administration) have shown that food of first-feeding larval anchovies becomes limiting when storms or drastic upwelling occurs and dilutes food aggregations. A complicating factor is that often nutritionally inadequate larval fish food can be overwhelmingly dominant in the larva's environment despite otherwise favorable oceanographic conditions (Lasker 1975, 1978; Scura & Jerde, 1977). This suggests that several conditions must be met for survival of first-feeding larvae; stability of the water column and aggregation of nutritionally suitable food organisms coinciding with the production of anchovy larvae in time and space.

As part of a study on DDT and PCBs, Scura & Theilacker (1977), using the low chlorinated hydrocarbon levels found in seawater, demonstrated that in the food chain leading to anchovy larvae, there is very small magnification of concentration. Rather they discovered that any bio-accumulation in larvae seems to depend on the direct partitioning of the chlorinated hydrocarbons between sea water and the larvae. Thus these chemicals probably have little direct effect on larval anchovy mortality in the sea. While the main spawning habitat of the northern anchovy is in the coastal waters adjacent to Los Angeles and the rest of heavily urbanized southern California, there is no evidence that dissolved pollutants of any kind affect the northern anchovy's reproductive success. On the other hand, studies by Hunter, Taylor & Moser (1978) at the Southwest Fisheries Center suggest that increased ultraviolet radiation due to slight reduction in the earth's ozone layer may be extremely deleterious to anchovy larvae.

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OCEAN VARIABILITY AND ITS BIOLOGICAL EFFECTS – REGIONAL REVIEW – NORTHEAST PACIFIC

Reuben Lasker

National Oceanic and Atmospheric Administration, National Marine Fisheries Service,
Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038, U.S.A.

A large number of environmental scientists and biological oceanographers in institutions bordering the northeast Pacific are studying the interaction between organisms at various trophic levels in the sea and changes in oceanographic conditions, including a major effort by the Coastal Upwelling Ecosystem Analysis (CUEA) program of the International Decade for Ocean Exploration (IDOE) and by a variety of other U.S. government supported projects to correlate ocean changes with biological variations. Among these is a NOAA-sponsored remote sensing study from aircraft and satellites using techniques that might be relevant to fishery oceanography. Upwelling events have occupied scientists up and down the margin of the northeast Pacific and correlations with larval fish survival, primary production, recruitment, growth and survival of crabs, and higher levels of the food web such as the distribution and abundance of migratory fishes have been examined. Historical analysis of variations in pelagic fish populations as far back as 150 years has been a recent area of investigation at Scripps Institution of Oceanography and correlations with past and present ocean conditions are being attempted. A recent study has shown that tree-ring growth and albacore migration can be tied together. In 1958, an unusual warming took place in the waters off California and recent studies have provided several interpretations of the cause of this phenomenon, the biological and oceanographic consequences of which have been recently documented. These and other aspects of research in the northeast Pacific on ocean variability and its biological effects are reviewed.

INTRODUCTION

In this paper, I have reviewed and selected for comment some of the newer approaches being taken to explain biological events in the northeast Pacific. Much of the information presented here is still in preparation and was obtained from the scientists themselves.

Currently, activity in the study of ocean variability is at a very high level in the northeast Pacific. Large programs such as NORPAX[1], OCSEAP[2], CUEA[3] and CalCOFI[4], sponsored respectively by the U.S. National Science Foundation (NSF), the U.S. Department of Interior's Bureau of Land Management, the International Decade of Ocean Exploration of NSF, and a California Department of Fish and Game – National Marine Fisheries Service (NOAA)[5] – Scripps Institution of Oceanography consortium, are currently in progress. Long-term monitoring of sea-surface temperatures by the National Marine Fisheries Service provides information used by oceanographers for studies of ocean variability and meteorologists for long-range weather predictions (Dickson and Namias, 1976). A NORPAX ship-of-opportunity program of vertical temperature profiles (expendable bathythermograph casts) and surface salinities exists from the U.S. west coast to Hawaii and has enabled Saur (1976) to monitor the seasonal and non-seasonal changes in surface temperature and salinity patterns, the sub-surface temperature structure, the heat content of the upper layers of the ocean, the boundaries between water masses and, by inference, the circulation of major currents in the northeast Pacific Ocean (Fig. 146).

OCEAN CLIMATE AND WEATHER

Cause and effect relationships are constantly being sought to explain and predict anomalous oceanic conditions and their consequent biological effects. For example, one interpretation of the intensive warming of the California Current from 1957 to 1959 is given in a recent paper by Jones (1975) who describes ad-

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[1] NORPAX – North Pacific Experiment.

[2] OCSEAP – Outer Continental Shelf Environmental Assessment Program.

[3] CUEA – Coastal Upwelling Ecosystem Analysis.

[4] CalCOFI – California Cooperative Oceanic Fisheries Investigation.

[5] NOAA – National Oceanic and Atmospheric Administration.

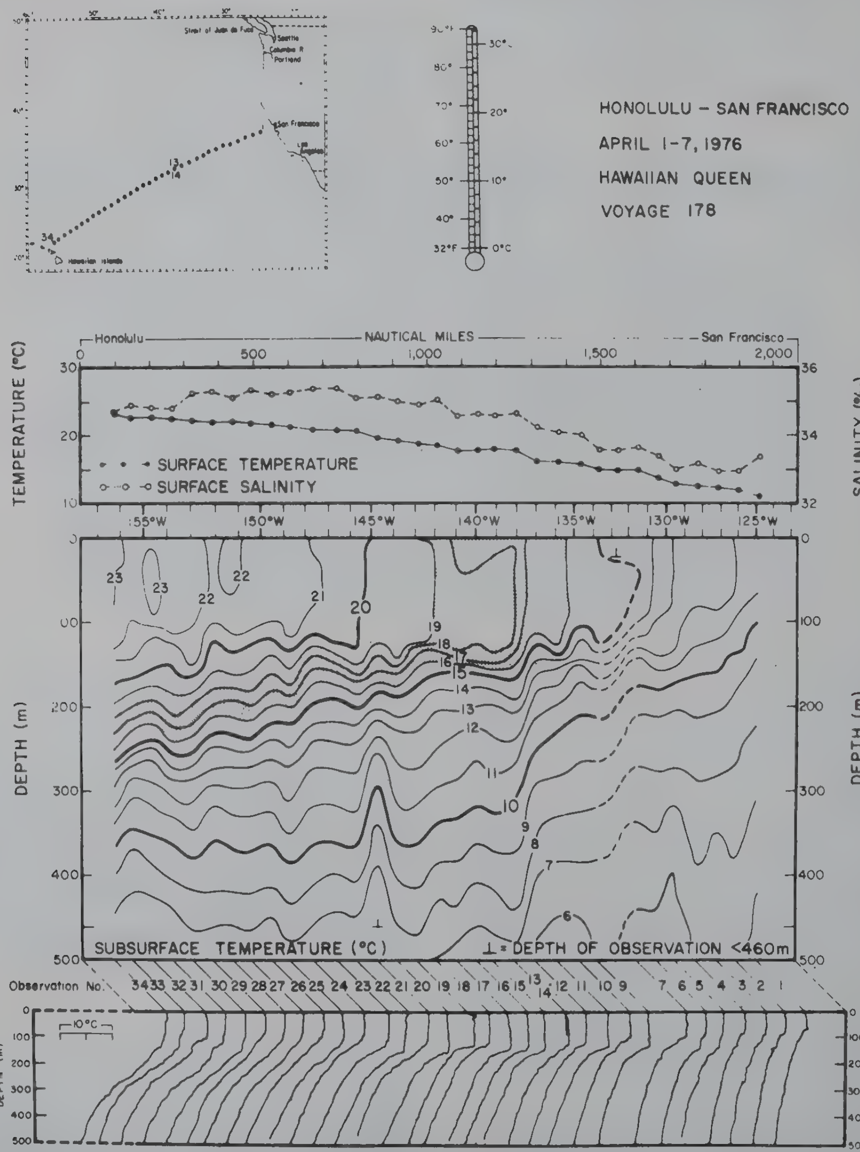


Figure 146. Example of ship-of-opportunity temperature profiles and surface salinity across the northeast Pacific and California Current (from Saur, 1976).

vection of warm water across the Pacific and links this to yearly changes in winter westerly winds over the north Pacific and to yearly changes in the Kuroshio Current. The ultimate cause of ocean and atmospheric changes, i.e., the qualitative and quantitative linkage between the ocean and the atmosphere is an intense area of study, particularly by Namias and his coworkers at the Scripps Institution of Oceanography. About the northeast Pacific Ocean, Namias (pers. comm.) writes that:

"During the last decade, empirical studies have shed a great deal of light upon the interrelationships between the northeast Pacific and the overlying atmosphere. In general, the sea and the air tend to act as a coupled system. In fact, linear regression equations have been derived which can specify the sea-surface temperature (SST) from the contemporaneous sea level pressure or 700 mb height or vice versa. Four term equations can explain roughly 80% of the variance. Although specifications derived in this manner are far from perfect, the essence of the large scale patterns is usually represented.

Auto-correlation studies have shown that SST anomaly (departure from a long-period mean) fields retain their characteristics over periods of several months to a year, while the atmospheric pattern correlations die away quite rapidly. The ocean acts as a conservative element due to its large heat storage capacity and relatively sluggish movement. There is a definite tendency toward recurrence or reemergence of cold season SST anomaly patterns during the following cold season. This recurrence is ascribed to storage of anomalously cold or warm water that is shielded by a shallow layer in summer but is stirred up to the surface by the increased wind stress during cold months. There is some evidence that SST anomalies are indicative of oceanic thermal anomalies extending to the main thermocline and even at times one or two hundred meters below this."

UPWELLING

Wide fluctuations in catch occur in almost all of the world's large commercial and sports fisheries and over a spectrum of time periods, from days to centuries. They are attributed to variations in fishing intensity and to changes in the natural environment. Also, environmental changes may vary widely in geographical extent from highly localized events to those of ocean-wide scale. The effects of these factors on the abundance and availability of commercial fish populations must be understood to achieve efficient harvesting and effective management.

Ultimately, biotic processes in the ocean will only be understood and predicted if we can predict with precision and timeliness what is going to happen to the ocean environment. In response to this need, oceanographers in the northeast Pacific have recognized the desirability of synoptic and timely oceanographic indices that could be used to correlate with biological events. Thus, Bakun of the Pacific Environmental Group of the National Marine Fisheries Service, Monterey, California, now provides, in addition to the work of Saur, monthly, weekly and daily coastal upwelling indices based on computations of Ekman transport divergence adjacent to the coastal boundary at 3° intervals along the west coast of North America. Monthly upwelling indices (Bakun, 1973) have been correlated with Dungeness crab fisheries off the west coast of the U.S. by Peterson (1973) and by Botsford and Wickham (1975). They found that increased upwelling favoured fishing success; lag times of $^1/_2$ year to $1^1/_2$ years indicated the effect to be on juvenile rather than on larval stages. Peterson explains the lag time as "probably a direct result of slow energy transfer through the pelagic environment to the benthos."

Parrish (1976) used this monthly upwelling index and a newer one, based on offshore surface layer divergence derived by Bakun and Nelson (in press), to analyse the Pacific mackerel fishery by regression analysis. Increased coastal upwelling in the vicinity of the spawning grounds just before or during the spawning season was found to favour recruitment, while increased convergence offshore appeared to be an inhibiting factor. Inclusion of these environmental factors in spawner-recruit functions resulted in models that describe nearly 80% of the variation in recruitment over the period 1946 to 1968 (Fig. 147).

Peterson and Miller (1975), studied year-to-year variations in the zooplankton of the Oregon upwelling zone within 10 km off the shore during 1969, 1970 and 1971. Peak abundances of zooplankton appeared during June and July of 1969 and 1970 when upwelling was strong in the inshore zone. 1971 was a relative weak upwelling year, and this correlated with low zooplankton abundance inshore. Neritic species were obviously abundant in 1969 and 1970 while some did not even appear 1971. Generally, offshore species were also numerically abundant in 1971, the poor upwelling year.

The CUEA program's objective has been to apply an interdisciplinary approach to biological productivity and its dependence upon coastal circulation in an upwelling regime. The research focuses around the development of realistic ecosystems models using the latest results from concurrent physical and biological field experiments conducted as part of the study. One of the most important objectives is the prediction of

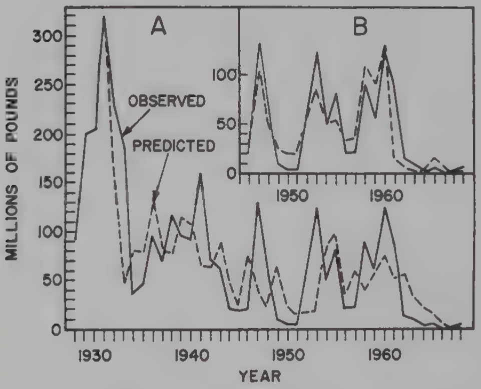


Figure 147. Observed and predicted recruitment of Pacific mackerel; A, Ricker sea level model; B, Ricker transport model (from Parrish, 1976).

fishing success from environmental changes being monitored.

Research of Inter-American Tropical Tuna Commission scientists in the CUEA program has been centered around the evaluation of remotely sensed observations (from aircraft and satellites) in ways that will be beneficial to fishery oceanography. Their recent work has suggested the possibility of using satellite temperature data from the scanning radiometer aboard NOAA satellites to obtain the optimum SST corresponding to tuna fish catch for different marine environments (Stevenson and Miller, 1974).

Infra-red satellite radiometry of SST has revealed that eddies and meanders of 100–300 km diameter in the California Current are coherent and persistent for days and sometimes weeks. Oceanic thermal fronts can be clearly seen when horizontal gradients exceed 0·5 to 1·0°C per kilometre (Bernstein et al, 1977) (Fig. 148). Plans for 1976 include the use and comparison of digital data from a geo-stationary satellite with data from a very high resolution radiometer at a time when tuna may be migrating through a region often expected to include a significant thermal front. Albacore, for example, seem to congregate at thermal fronts.

MIGRATION OF ALBACORE AND TRANSITION ZONE OCEANOGRAPHY

Real-time readout of SST and determination of frontal systems by satellite is closely related to work being done by Laurs and Lynn (1977) on seasonal migration of the albacore *Thunnus alalunga*. In 1972, 1973 and 1974, broad scale surveys were carried out in the northeast Pacific with intensive oceanographic sampling and a substantial fishing effort. Their results demonstrated that the shoreward migration of albacore is associated with the transition zone between the cool, low salinity Pacific sub-arctic water to the north and the warm, highly saline eastern north Pacific central water to the south. Transition waters are found in a zonal band across the north Pacific bounded by sharp horizontal gradients in temperature and salinity. Laurs and Lynn (1977) show convincingly that when the transition zone is distinct, it concentrates migrating albacore, and that they stay in the zone for a few weeks and catch rates are predictably high (Fig. 149). When, as in 1974, the transition zone is broad and indistinct, the albacore occur over a much broader area during their migration and move rapidly inshore, staying no more than several days in the weak transition zone (Fig. 150). Laurs and Lynn (1977) postulate that the important factors responsible for the albacore's response are ambient temperature preferences, food availability, and thermal gradients as these affect body thermoregulation by the albacore. They believe these are integrated and superimposed on the innate drive of the fish to migrate across the north Pacific Ocean.

Saur (1976), in his analysis of the April 1976 transition zone development, predicted that it would be weak in the summer months. Laurs (pers. comm.) says that this was indeed the case and the albacore were, as predicted, spread over a large area of the ocean in June and travelled through the zone rapidly.

ANCHOVY RECRUITMENT

Strong coastal upwelling may be detrimental to recruitment for some fish species. Lasker (1978) gives evidence based on field and laboratory experiments with first-feeding northern anchovy (*Engraulis mordax*) larvae that the break-up of dense patches of properly-sized food particles and the substitution of small diatoms for easily seen and ingested dinoflagellates was inimical to anchovy larval survival in California waters. Because of the clear-cut and rapid phytoplankton succession and the onset of upwelling in 1975 during the northern anchovy's spawning season (Figs 151 and 152), Lasker predicted that the 1975 northern anchovy year class would be a relatively poor one. At the time of writing (August 1976) all indications are that the 1975 year class will be a bad one compared with those preceding it. The timing of the onset, the duration and the areal extent of upwelling along the California and Baja California coast, therefore, may be important predictors for recruitment of clupeids.

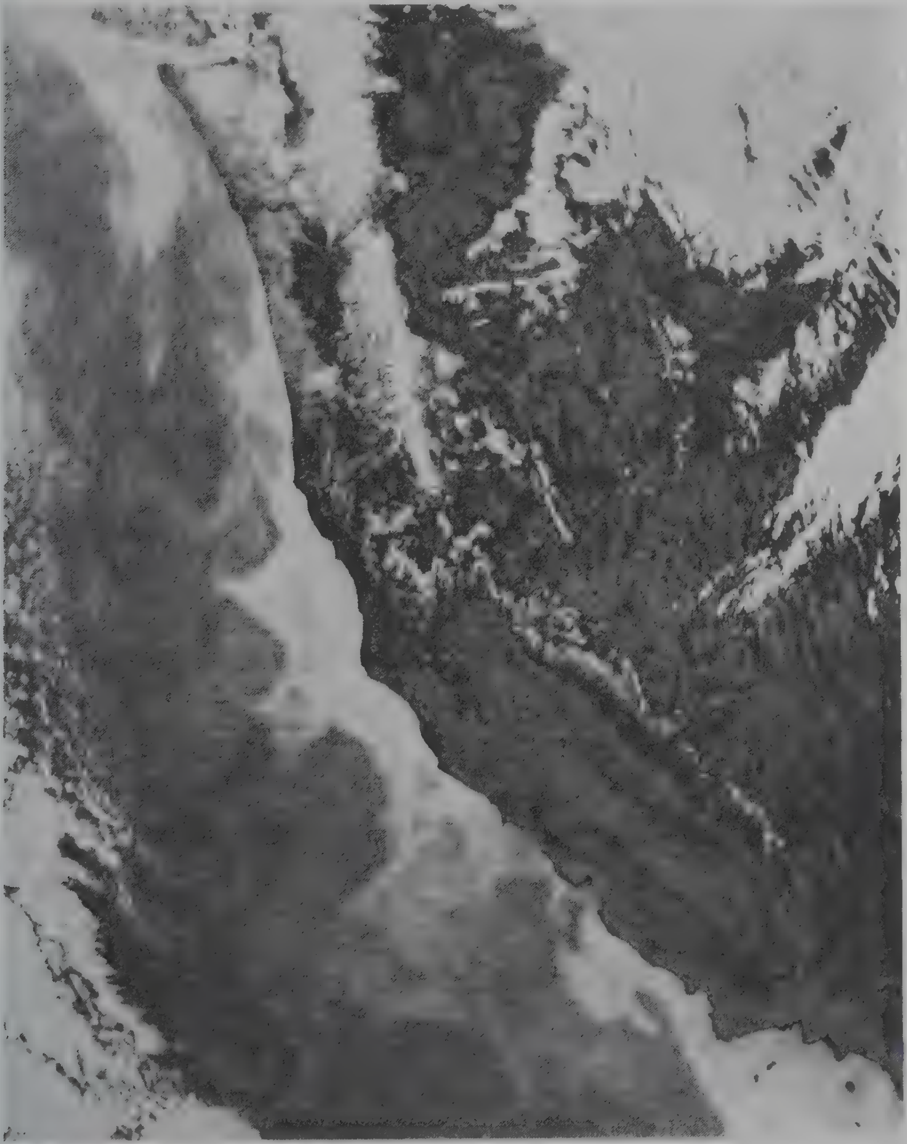


Figure 148. Infra-red photograph of the west coast of North America, 11 September 1974, showing large-scale meanders of the California Current and coastal upwelling. Dark ocean areas are warm, light are cold. Feathery light areas to the left of the photograph are clouds. (Photo courtesy of Merritt Stevenson, Inter-American Tropical Tuna Commission, La Jolla, California, and the National Environmental Satellite Service Field Station, Redwood City, California.)

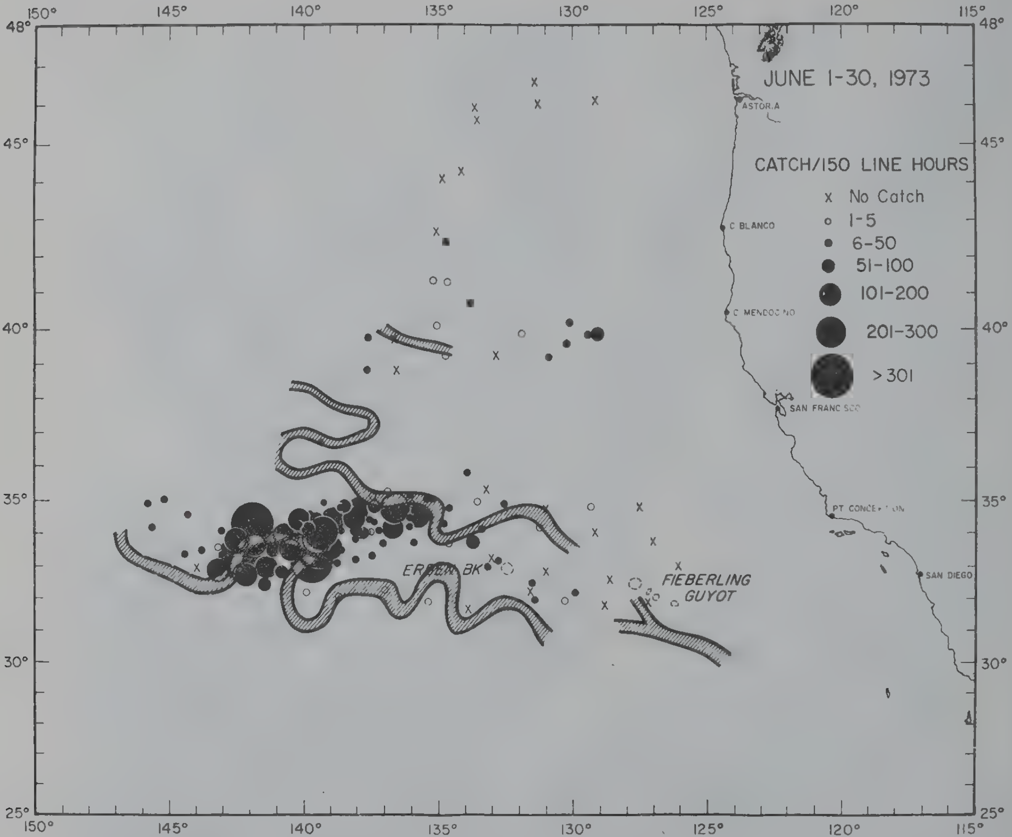
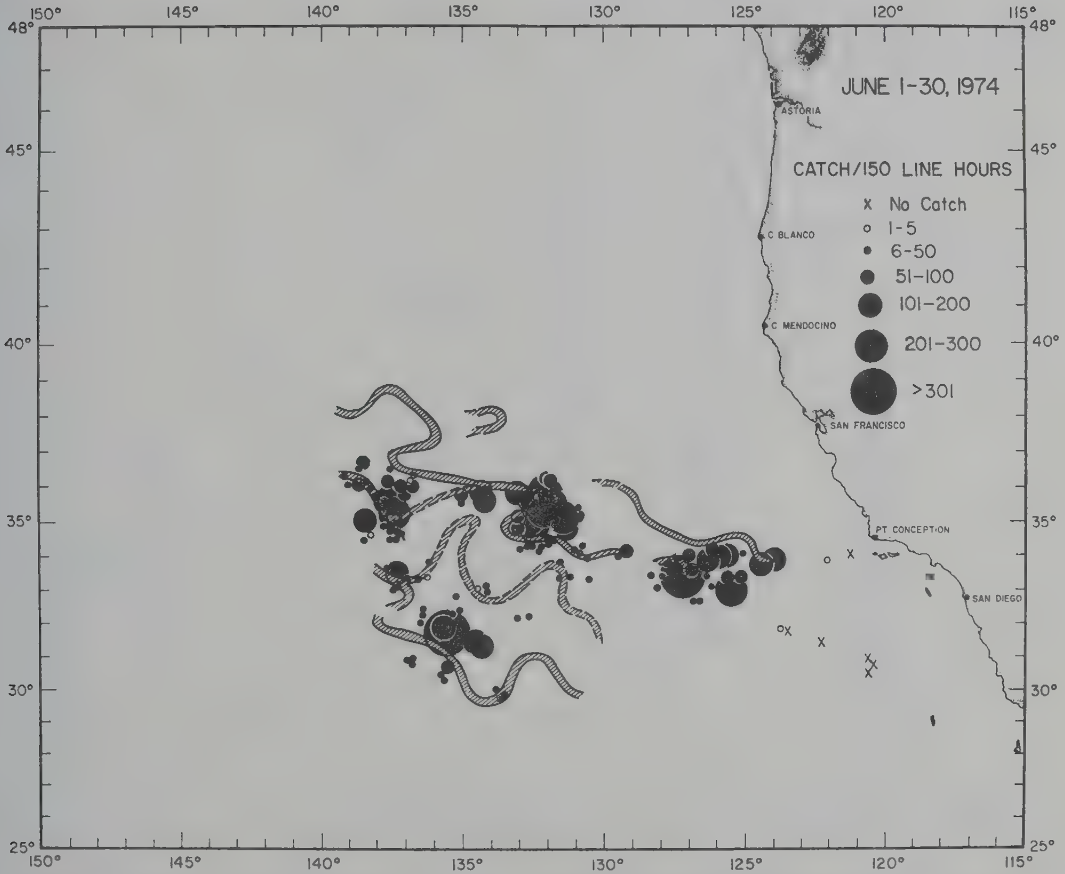

JUNE 1-30, 1973
ASTORIA
CATCH/150 LINE HOURS
x No Catch
○ 1-5
● 6-50
● 51-100
● 101-200
● 201-300
● >301
C BLANCO
C MENDOCINO
SAN FRANCISCO
PT CONCEPTION
SAN DIEGO
ERBEN BK
FIEBERLING GUYOT
150°
145°
140°
135°
130°
125°
120°
115°
48°
45°
40°
35°
30°
25°

Figure 149. Albacore catch per 150 line-hours by American Fishermen's Research Foundation's charter vessels and locations of fronts delineating Transition Zone waters during 1–30 June 1973 (from Laurs and Lynn, 1977).

Other oceanographic factors may have to be known for accurate anchovy year class prediction. For example, in 1975, prior to upwelling, conditions in the Southern California Bight favoured the growth and multiplication of the armoured dinoflagellate *Gonyaulax polyedra* which is used as food by anchovy larvae. Laboratory experiments (Scura and Jerde, 1977) showed that this dinoflagellate is a poor food for anchovy larvae. Thus, the additional factor of the dominance of nutritionally poor larval anchovy food may be important in predicting larval anchovy survival. Understanding the relationship between oceanographic variability and phytoplankton species succession, therefore, becomes an important area of study. Eppley and Harrison (1975) summarized work on causative mechanisms for red tides. From available evidence they show that dinoflagellate blooms are associated with steep, shallow thermoclines. When nutrients are low in the shallow mixed layer (< 10 m), but high underneath the thermocline, the vertical migratory range of the dinoflagellates enables these to obtain the nutrients they need. Coupled with an unusual nitrogen metabolism (e.g., dark assimilation of nitrates; Harrison, 1976) this provides dinoflagellates with an advantage over coastal diatoms when a shallow mixed layer exists.


JUNE 1-30, 1974
CATCH/150 LINE HOURS
x No Catch
○ 1-5
● 6-50
● 51-100
● 101-200
● 201-300
● >301
ASTORIA
C BLANCO
C MENDOCINO
SAN FRANCISCO
PT CONCEPTION
SAN DIEGO
150°
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40°
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30°
25°

Figure 150. Albacore catch per 150 line-hours by American Fishermen's Research Foundation's charter vessels and locations of fronts delineating Transition Zone waters during 1–30 June 1974 (from Laurs and Lynn, 1977).

FISHERIES ANALYSIS

Environment Canada scientists have looked at British Columbia fisheries with the objective of developing predictive indices for sizes of stocks and movement of fish to aid in managing the fisheries. Because there is not very much known about the interaction of trophic levels in this region, Wickett of the Pacific Biological Station, Nanaimo, B.C., has applied multiple regression statistics to assess the fraction of variance of annual catches of various species of fish or in annual changes of migration routes due to various indices of ocean variability for which long-term data sets exist. For example, he found a predictive relationship between the percentage of Fraser River sockeye salmon that return to their river by the passages between Vancouver Island and the mainland if he considered annual variations in the amount of Fraser River water discharged into the ocean and the wind stress forcing the freshwater against the coast and the north end of Vancouver Island; 71% of the variability in the percentage of returning salmon could be accounted for by using these two indices (Wickett, 1975). Similarly, rainfall at spawning, hours of bright sunlight, and the time when fry are moving offshore were all correlated with the even-year stock size of pink salmon along the central British Columbia

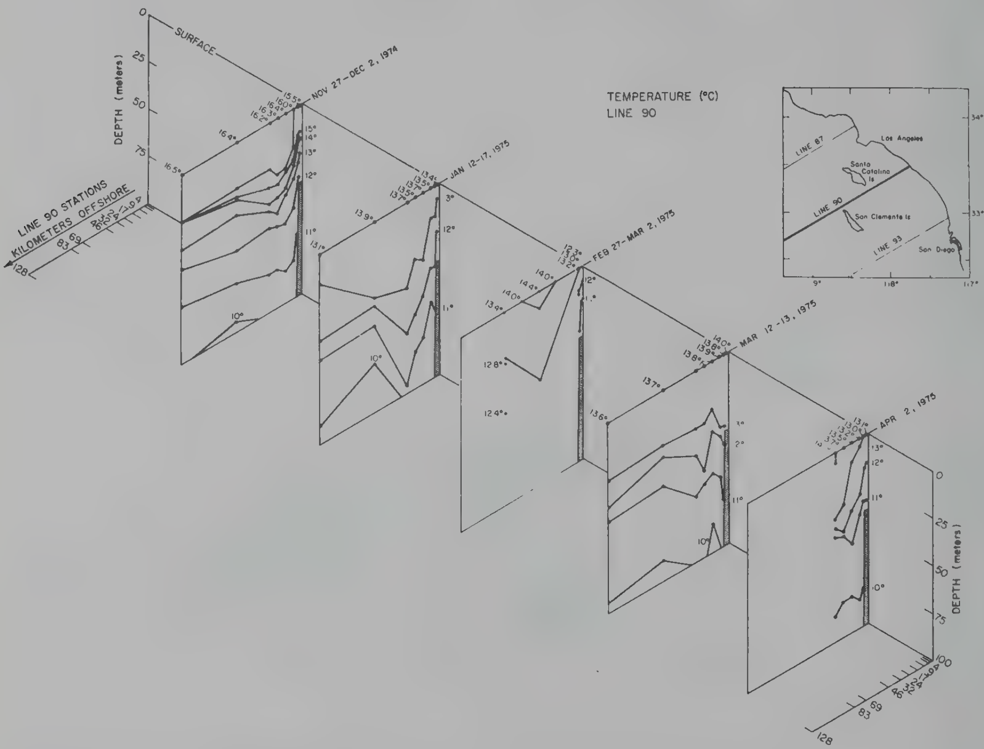

Figure 151. Temperature profiles during five cruises from November 1974 to April 1975. Line 90 extends from Dana Point to offshore between Santa Catalina and San Clemente Islands (from Lasker, 1978).

coast, and 89% of the variance in stock size from 1930 to 1974 could be accounted for in this way (Wickett, pers. comm.) (Fig. 153).

An identification of the basic principles that determine periodic phenomena in the sea has been attempted by Favorite and Ingraham (1976) who have found that during periods of sunspot maxima (approximately every 11 years), there is a shift in the mean winter position of the center of the Aleutian low pressure system from the Gulf of Alaska to the western Aleutian Islands. This results in a reduction of the mean cyclonic, windstress transport in the Gulf of Alaska by about 20%. While the authors have not yet been able to correlate this shift with any biological events, they believe there is evidence to suggest that the 11-year sunspot cycle is related to a 5- to 6-year sea-surface temperature maxima-minima cycle in the northern north Pacific Ocean which is "largely in phase" with mean sea level maxima in the Gulf of Alaska. This latter phenomenon may, in turn, be correlated with dominant year classes of herring, e.g., in 1953 and 1958, years of temperature maxima in southeastern Alaska.

HISTORICAL OCEANOGRAPHY

Several unusual studies which might be termed "historical oceanography" have been done in the northeast Pacific over the last few years. The first of these by Soutar and Isaacs (1974) provided biomass estimates of pelagic fish over the past 180 years, as indicated by fish scale deposition in anaerobic basins off California and Baja California because anoxia prevents decomposition of the organic scales. Using

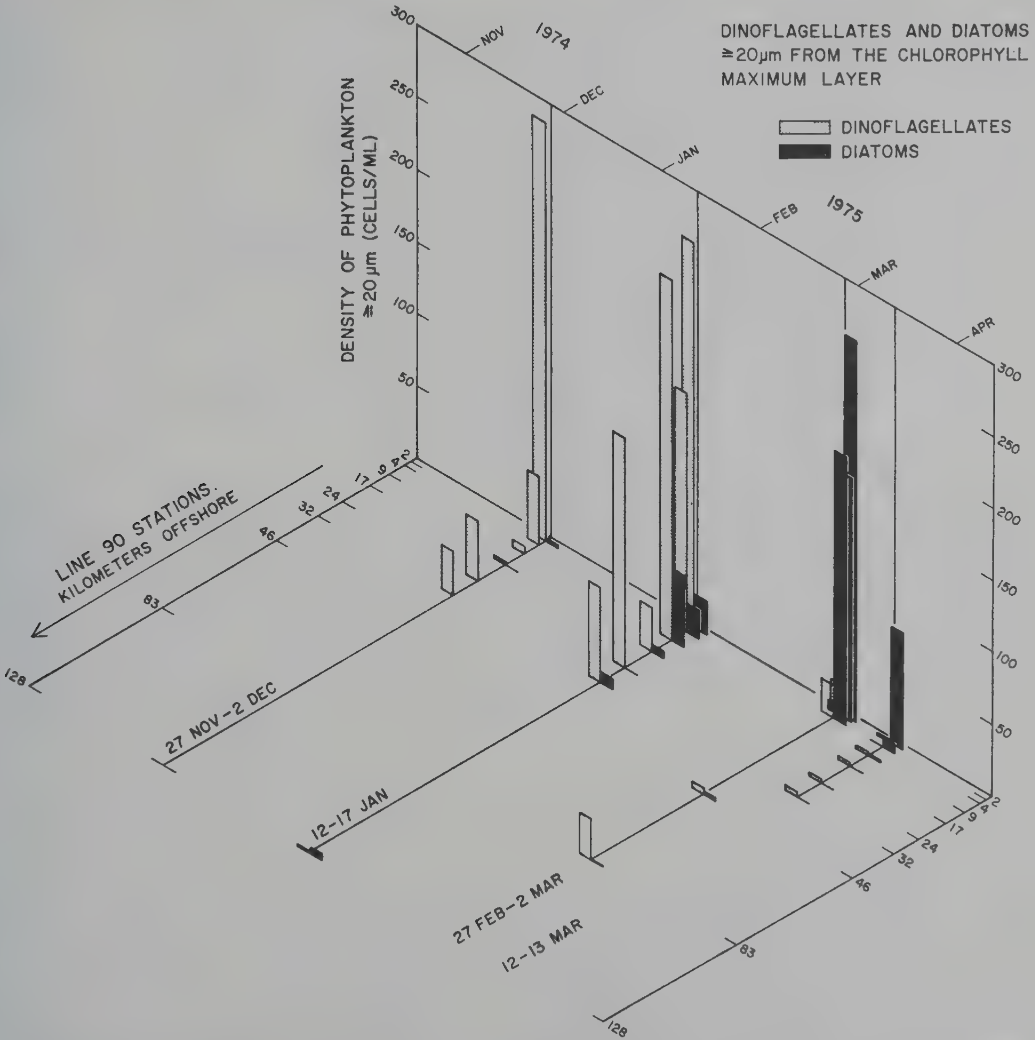

Figure 152. A comparison of diatom and dinoflagellate abundance along CalCOFI line 90 (see Fig. 151) over the anchovy spawning season (from Lasker, 1978).

over 80 meteorological recording stations in southern California, these authors have now developed seasonal rainfall indices for Santa Barbara, Los Angeles, San Bernardino and San Diego, for the years 1865 to 1970. The four indices were found to be closely related and reflected the regional storm systems generated in the north Pacific that are the source of nearly all the rainfall run-offs in coastal southern California. A temperature index has also been constructed, although from fewer stations; the high degree of correlation in temperature from these reflects the regional extent of temperature anomalies (Namias and Born, 1970)

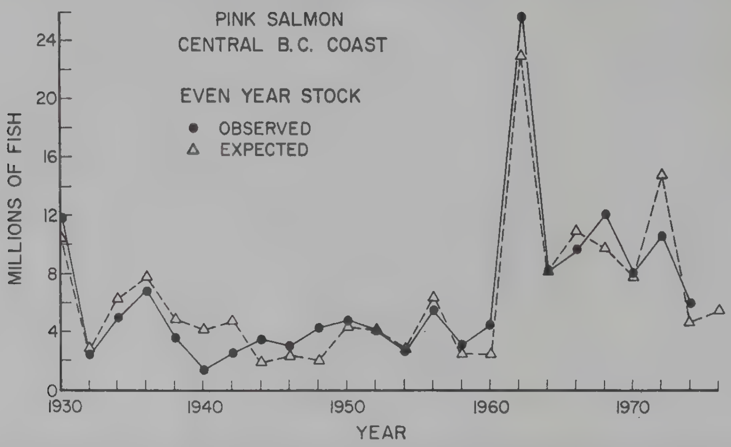

Figure 153. Predicted and observed pink salmon even-year stock from central British Columbia (Wickett, pers. comm.).

and permitted Soutar and Isaacs to construct a central California seasonal temperature index. They have found that a correlation matrix set-up for temperature, rainfall, tree growth and the thickness of sediments in anaerobic basins adjoining California demonstrates the dominant effect of rainfall on both tree growth and on sedimentation and that undisturbed deep oceanic sediments may be used, therefore, to interpret the paleoclimate.

Similarly, Poelchau (1974) developed a temperature-of-the-ocean index in the northeast Pacific by using silicoflagellates as bioclimatic indicators. Soutar is currently examining over 100 forms of radiolarians and silicoflagellates to assess regional patterns of climatic variability around Southern and Baja California.

Because albacore migration is related to the thermal structure of the eastern north Pacific Ocean and the catch estimated from landings off the U.S. west coast

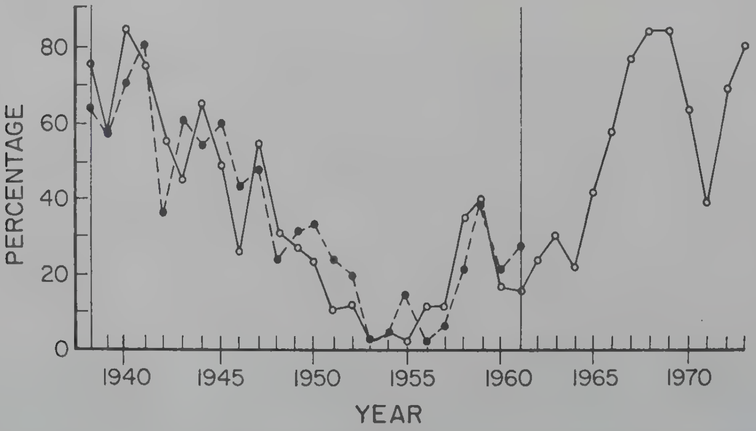

Figure 154. Percentage of the total north American west coast albacore catch taken north of San Francisco, estimated from landings data (——) and percentage catch taken north of San Francisco derived from the calibration equation applied to tree-growth data over the dependent data periods (– – – – –) (from Clark et al, 1975).

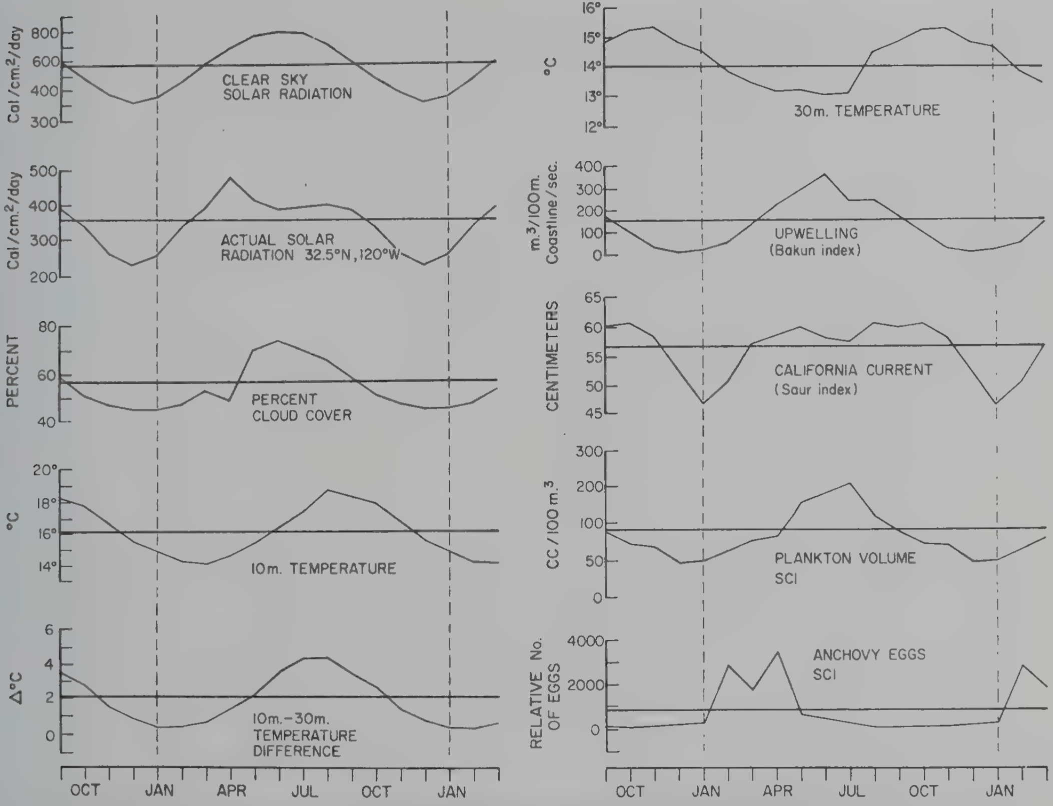

Figure 155. Seasonal cycles of physical and biological parameters in the Southern California Bight (from Lasker and Smith, in press). SCI = Southern California Inshore region.

is related to the extent of the northward migration along the west coast, Clark et al (1975) believed that the growth of conifers in western North America and the catch of albacore would both be influenced by the same air-sea interaction processes. They found a correlation between patterns of tree ring growth and albacore catch and used this to reconstruct the variability in north-south distribution of migrating albacore for the past 250 years (Fig. 154).

TIME SERIES

Time series of oceanic and biological parameters have had their protagonists and antagonists, but without these series, the magnitude and extent of important single events and deviations from the "average" conditions would go undiscovered. The only ocean temperature and salinity time series available over long periods of time in the California region have been from shore stations, notably from the Scripps Institution of Oceanography's pier in La Jolla and a number of similar stations north of San Diego. CalCOFI oceanographic and biological multi-ship surveys began as early as 1940, but complete data sets are available only so far for the years 1951 through 1969.

Some short-term and long-term data for the California inshore region alone, which includes the Southern California Bight, have been summarized by Lasker and Smith (in press) (Fig. 155). These show the mean timing of atmospheric, oceanic and biological events. Anchovy spawning generally begins when the California Current has slackened, and upwelling is at its

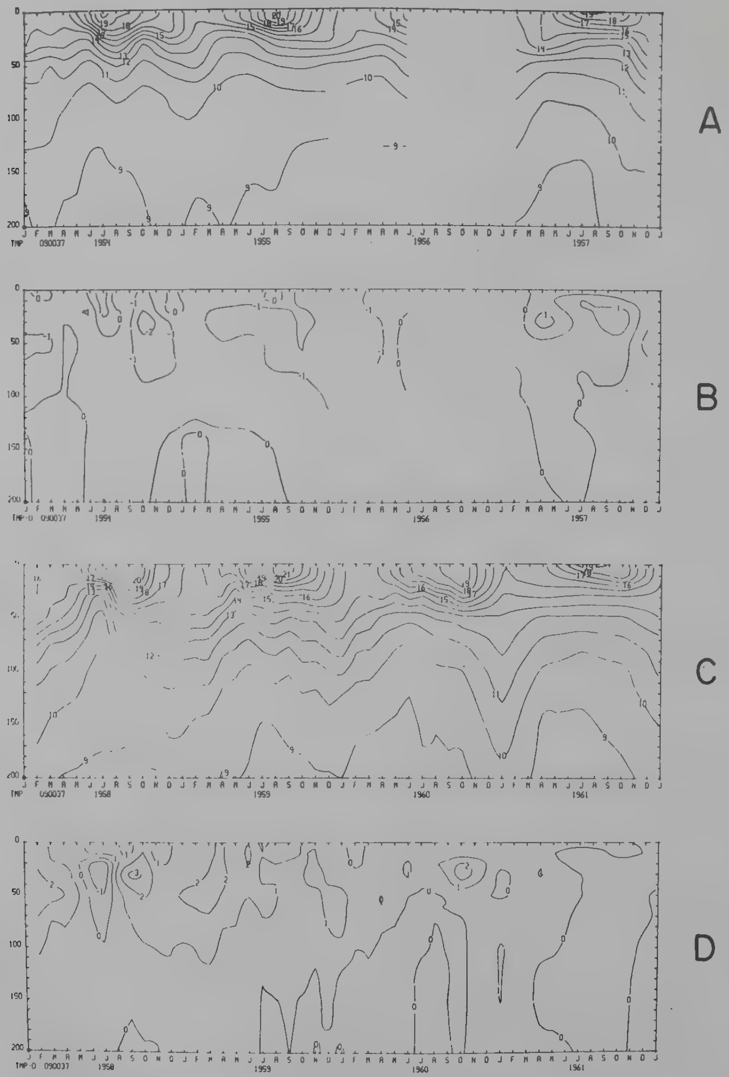

Figure 156. Time series (1954 through 1961) of temperature with depth (A and C) and temperature anomalies (B and D) at 33°11′N 118°22·5′W in the Southern California Bight. (CalCOFI data compiled by L. E. Eber).

lowest ebb. Until now, however, this mass of temporal data, which encompasses horizontal and vertical physical and chemical changes in the California Current, has been inaccessible because it was not in a useable and retrievable form. Efforts to rectify this situation are now being made at the Southwest Fisheries Center in La Jolla. Figure 156 is an example of temperature with depth for a single station 36 miles off Pt. Dume, California. This clearly shows the anomalies for the 1957–1959 warm-water years. Oceanographic data from the entire CalCOFI area are now available for analysis by fishery biologists to see if correlations can be made between physical parameters and fluctuations in biotic populations (Eber, 1977). Biological information to correlate with oceanic changes is also being made available in easily usable forms, e.g., tables and graphs. For example, Smith (pers. comm.) has just completed a 1951–1969 time series of larval anchovy abundance showing how mortality differs from year to year between larval size classes.

From a 14-year time series (1949–1962) produced for the north Pacific by Eber et al (1968), Eber (1971) traced temperature anomaly fields in the north Pacific and identified the existence of a standing wave in the current structure which could affect the partitioning of the West Wind Drift Current as it approaches the north American coast and splits into northward and southward flowing branches. A southward excursion of the current is reflected in a strong negative anomaly offshore; a swing back northward appears as a positive anomaly in the Gulf of Alaska. This would have the effect of reducing the normal flow of cold water into the California Current allowing it to become warmer.

Zooplankton volumes from CalCOFI surveys were related by Wickett (1967) to mean meridional Ekman transport for January to August, 1000 miles upstream of the CalCOFI survey area for the years 1952 through 1959. Greater outflow of high nutrient sub-arctic water into the California Current resulted in higher zooplankton volumes. Less than normal flow of the California Current in 1957–1958 seems consistent with this. Colebrook (1976) applied principal component analysis to zooplankton distributions for 17 major taxonomic categories from CalCOFI collections for the period 1955 to 1959. He showed that a large proportion of the variability in biomass of zooplankton could be associated with hydrographic events. The upstream-downstream distribution and abundance of zooplankton biomass was determined to be the first principal component by Colebrook while onshore-offshore distribution and abundance was found to be the second principal component. There seems little doubt that the reduction in zooplankton biomass connected with the first principal component in 1958–1959 was in some way related to the anomalous change in temperature which began off southern California in 1957, its northward spread along the western north American coast in 1958 and persistence into 1959, and the associated reduction in flow southward out of the sub-arctic circulation of the north Pacific. The second component, Colebrook believes, was strongly influenced by fluctuations in coastal upwelling.

Using factor analysis to examine its multivariate structure, Hemingway (in prep.) has described the California Current from 21 physical, chemical and biological variables taken in 1969 from 216 stations. Three physical regimes were described numerically, i.e. mixing, upwelling and thermal stratification. He found that nutrients and high chlorophyll due to phytoplankton production was associated with mixing and upwelling regimes whereas first-feeding anchovy larvae were associated with upwelled and thermally stratified water, but not with mixing regimes.

CONCLUSION

This brief review of selected activities in the northeast Pacific Ocean illustrates a steady and encouraging progress in understanding how biological changes are affected by the ocean environment. There is a strong momentum for research on ocean variability in this geographic area and a continuing awareness of its importance.

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THE RELATION BETWEEN OCEANOGRAPHIC CONDITIONS AND LARVAL ANCHOVY FOOD IN THE CALIFORNIA CURRENT: IDENTIFICATION OF FACTORS CONTRIBUTING TO RECRUITMENT FAILURE

Reuben Lasker

National Oceanic and Atmospheric Administration, National Marine Fisheries Service,
Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038, U.S.A.

Evidence is offered in this paper to suggest that monitoring the extent and aggregation of potential larval fish food particles over a spawning season along with pertinent environmental parameters may be a practical way to predict the relative degree of pelagic fish recruitment and the strength of the resultant year class.

To discover the extent, both horizontal and vertical, of larval anchovy feeding areas and how these change with time and a variety of oceanographic and meteorological conditions, a survey of inshore and offshore particle distribution was made off southern California from September 1974 through September 1975. The temporal and spatial picture of the anchovy larva's micro- and macro-environment was expected to suggest whether conditions were good for larval anchovy feeding and hence whether good or bad recruitment might be expected on the basis of larval food distribution.

In an earlier study it was shown that it is possible to establish whether a body of water is a good or poor feeding ground for first-feeding larval anchovy, *Engraulis mordax*. Sufficiently high numbers (> than 30 particles/ml) of proper-size food organisms (cells approximately 40 µm diameter) have to be present for successful feeding.

Food was abundant within 5 km off the California shore in chlorophyll maximum layers prior to January 1975. Gyral circulation caused a widespread distribution of food throughout the Southern California Bight in January. In February 1975, a major upwelling event occurred in this area. The proper-size food particles, mostly dinoflagellates, which were abundant before the upwelling, were dissipated because of it. Smaller particles in the form of a variety of diatoms supplanted the dinoflagellates. Laboratory and field experiments have shown that regardless of their concentration, small diatoms do not provide the caloric requirements of first-feeding anchovy larvae. Upwelling continued through the early spring and summer months of 1975 and diatoms persisted. Early spring was the end of the anchovy spawning season. The data suggest that the timing of onset and the duration of upwelling are crucial determinants for survival of larvae and the resultant year classes of the northern anchovy.

INTRODUCTION

It is known from well-studied fisheries, e.g., the Atlanto-Scandian herring (*Clupea harengus*) that there is often no correlation between the size of a spawning stock and the size of its resultant year class (Hjort, 1926). Although pelagic and benthic fishes can produce enough eggs to replace their own individuals lost by natural and fishing mortality, often there are population collapses which cannot be correlated with the amount of spawning. On the other hand, there are also examples of exceptionally large pelagic fish year classes which have been produced from relatively small spawning stocks (Simpson, 1956).

Even when no fishery exists, great changes in the magnitude of pelagic fish populations may occur. For example, large fluctuations in the population size of the Pacific sardine (*Sardinops caerulea*=*S. sagax*) and northern anchovy (*Engraulis mordax*) in the California Current have taken place recently (Smith, 1972) as well as over the last 150 years, as shown by Soutar and Isaacs (1974) from sedimentary records off California.

An estimation of recruitment into an upcoming year class from the statistical information available on the size of the spawning stock can be unreliable. This was particularly evident when the Peruvian anchoveta (*Engraulis ringens*) fishery collapsed in 1973. The catch of anchovies fell drastically below the previous years' catches, from 10 million metric tons annually to less than 5 million metric tons. The panel of experts on stock assessment of the Peruvian anchoveta recognized that two years of poor recruitment touched off the collapse of that fishery, in common with the decline and disappearance of other formerly

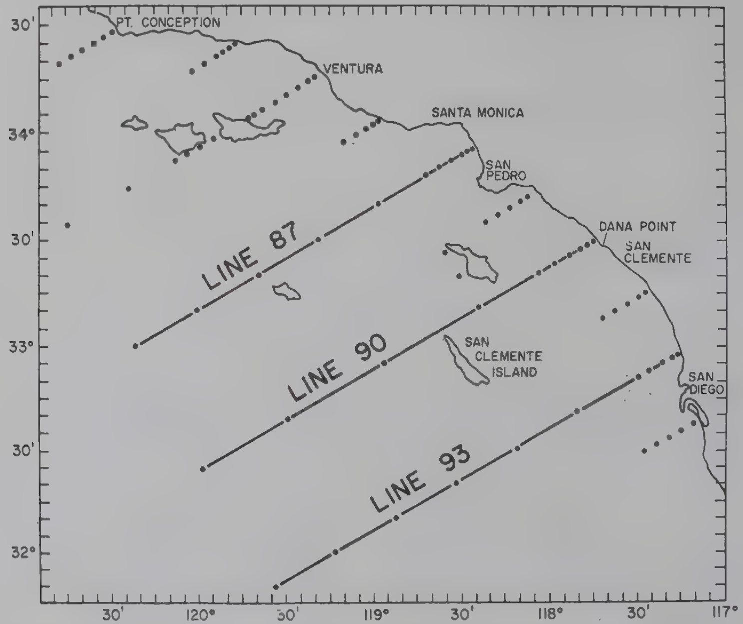

Figure 182. Basic sampling stations for the Southern California Bight. Inshore stations are located 1, 2 and 4 km from the shore.

great fisheries such as the Atlanto-Scandian herring, the Pacific sardine, the Hokkaido herring and the Japanese sardine (Murphy, 1974).

Thus despite the ability of fishery scientists to recognize the failure of recruitment into a fishery after-the-fact, there is still a lack of understanding of the mechanisms that determine year-class strength in pelagic fish populations. To manage a fishery, fishery scientists would like to be able to predict whether and to what degree any particular spawning will result in successful recruitment. For maximum economic exploitation, managers would like to know how small a spawning stock may be to ensure subsequently a reasonably large year class.

In an earlier study (Lasker, 1975), I showed from a combination of laboratory and field work that there are criteria for characterizing a body of water as a good or poor feeding ground for first-feeding larval anchovy, *Engraulis mordax*. The present study describes the results of an environmental survey of the California Current based on this earlier work and delimits the area and time when first-feeding anchovy larvae can feed sufficiently to ensure survival. Evidence is offered to suggest that monitoring the extent and aggregation of potential larval fish food particles over a spawning season along with selected environmental parameters may be a practical way to predict the relative degree of anchovy recruitment and the strength of the resultant year class. Sette (1943) in a prescient article anticipated that a meteorological-oceanographic connection might be used to predict recruitment. Data given in this paper add strength to his premise.

THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

The northern anchovy (*Engraulis mordax*) spawns in the California Current, a broad sluggish (12 km/day) southward moving current along the U.S. west coast and Baja California, Mexico (Kramer and Ahlstrom, 1968) which is characterized by gyres (Jones, 1971). The central sub-population of the northern anchovy, recently estimated at 3 to 5 million metric tons in its spawning area of 80000 km^2 (Smith, 1972) in 1974–1975, supported a 40000 metric ton

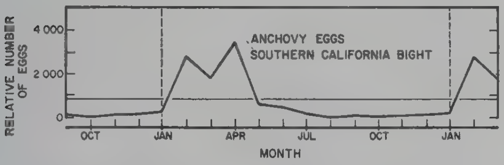

Figure 183. Annual spawning cycle (appearance of anchovy eggs) in the Southern California Bight; 8 year average from 1953 to 1960 (from Lasker and Smith, in press).

fishery in Mexico and a 110000 metric ton fishery in California. Mexico has announced its intention to exploit this resource at 500000 tons annually (Keir and Melcer, 1975).

The anchovy is highly fecund and a mature female is capable of producing thousands of eggs at a single spawning. Yet the larvae produced from eggs die at an exponential rate in the sea. Lasker and Smith (in press) have shown that on the average there is only 0·06% survival at 20 days of larval age for the northern anchovy, with 40 or more additional days still to go until metamorphosis, depending on temperature. Various explanations for this enormous mortality have been suggested. Hjort's hypothesis (1914), that for a larva to survive it must have the correct food in the right density when it starts to feed and that the success of a subsequent year class depends on this, has not been disproven and continues to be one of the most reasonable explanations for differential larval survival (May, 1974). Hjort's idea as restated by May (1974) is that the strength of a year class is determined by the availability of planktonic food shortly after the larva's yolk-sac has been exhausted.

Laboratory work on northern anchovy has shown that relatively high densities of food particles are needed by first-feeding anchovy larvae to account for: 1) their inefficient ability to capture food during the first few days of feeding (Hunter, 1972), 2) their relatively high metabolic requirement (Vlymen, 1974),

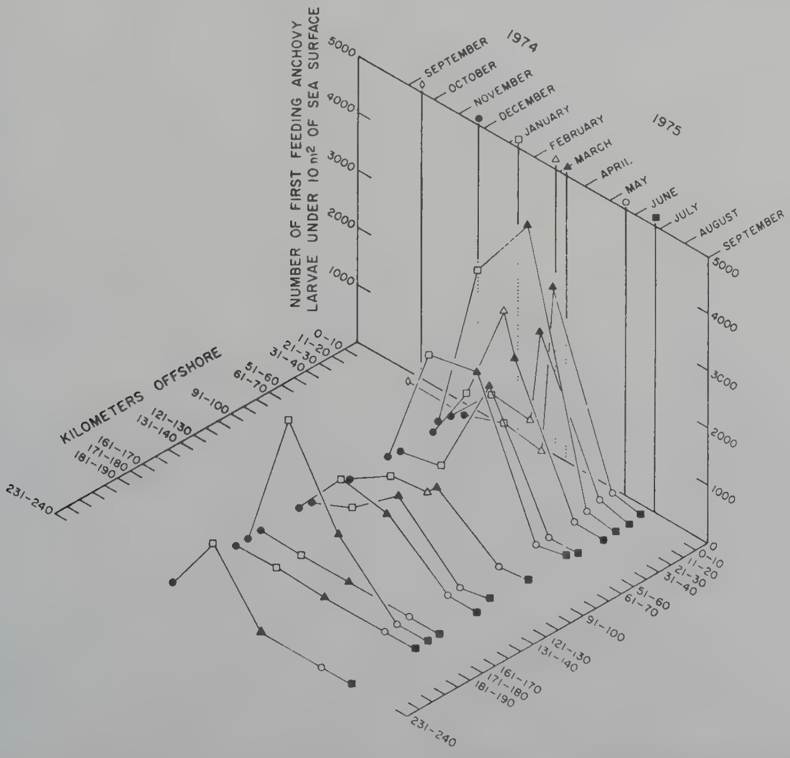

Figure 184. Spatial and temporal distribution of first-feeding northern anchovy larvae in the Southern California Bight and offshore zone. Symbols identify particular cruises as indicated on the abscissa.

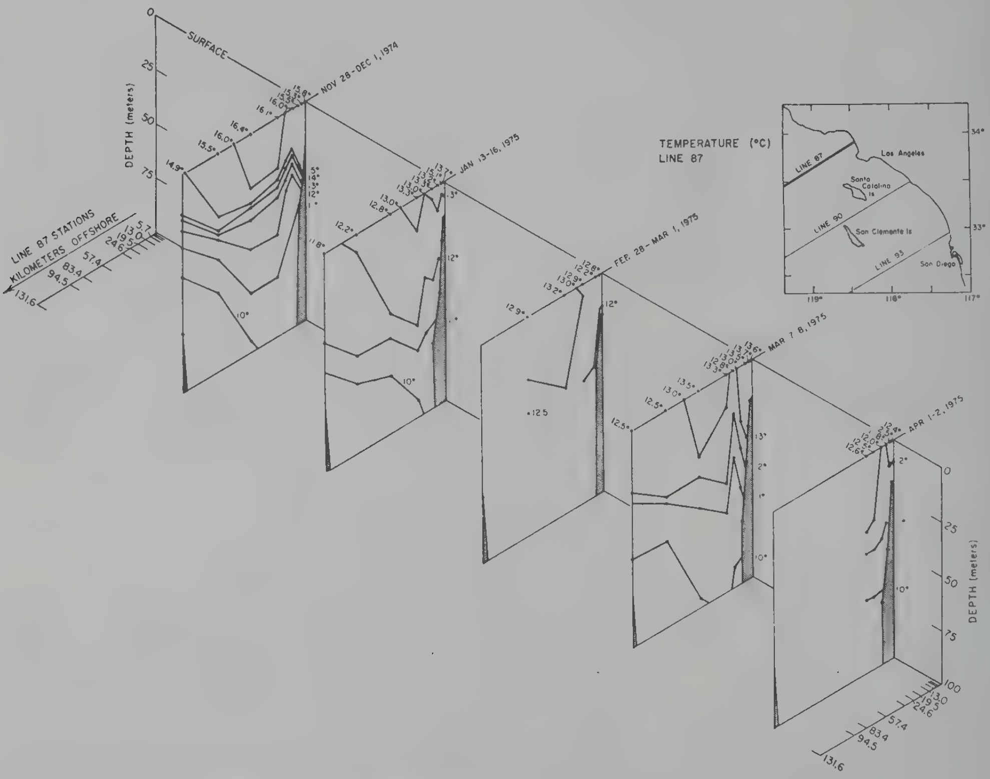

Figure 185. Temperature profiles during five cruises from November 1974 to April 1975. Line 87 extends from Santa Monica Bay, California to offshore.

3) a small mouth size restricting the maximum particle size that can be taken, and 4) the cessation of feeding at night (Arthur, 1976). Hunter (in press) has calculated that approximately 230 food particles of about 50 µm in diameter (e.g., the size of the unarmoured dinoflagellate, *Gymnodinium splendens*) would have to be consumed per day by a first-feeding anchovy larva to meet its metabolic requirement.

TEST AT SEA OF HJORT'S HYPOTHESIS

In an earlier investigation (Lasker, 1975), laboratory-hatched first-feeding anchovy larvae were allowed to feed in natural sea water in March and April 1974 and in various densities of *Gymnodinium splendens* in the laboratory. Both experiments showed that a full or partial filling of the gut over an 8-hour period required between 20 and 40 cells per millilitre in the larva's environment. Cells smaller than 30 µm in "effective diameter"[1] were taken only occasionally (Lasker, 1975). Sufficiently high numbers of proper-size food organisms were found chiefly in well-developed chlorophyll maximum layers adjacent to the California coastline. A stormy period was effective in eliminating the chlorophyll maximum layer and in diluting the potential food organisms (in this case the unarmoured dinoflagellate, *Gymnodinium splendens*) below the critical density needed for feeding. An unusual finding was that the dinoflagellate population extended for at least 100 km along the shore.

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[1] Coulter Counter (Model Ta) was used to record the volumes of individual particles. Despite the fact that particles are varied in shape, in this study, sizes were recorded by "effective diameter" as if all particles sampled were spheres.

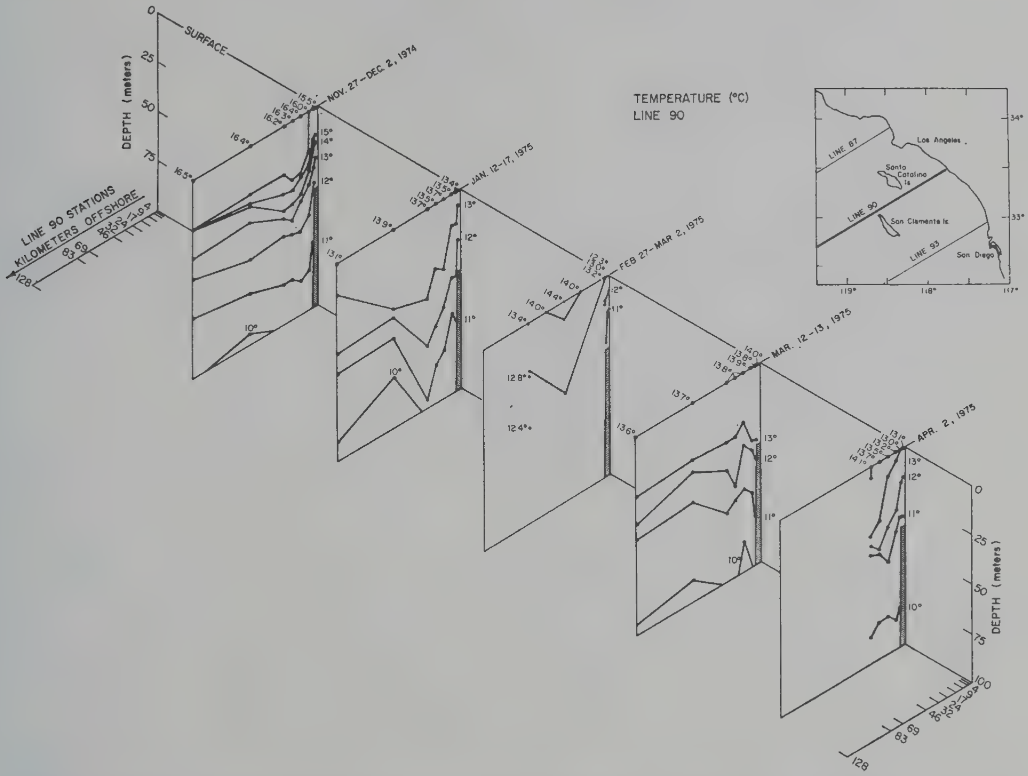

Figure 186. Temperature profiles during five cruises from November 1974 to April 1975. Line 90 extends from Dana Point, to offshore between Santa Catalina and San Clemente Islands.

The seaward extent of this huge "patch" was not ascertained (Lasker, 1975; Kiefer and Lasker, 1975).

The threshold for larval anchovy successful first-feeding was therefore defined as the presence of at least 30 cells/ml of particles 30 to 50 μm in effective diameter. Successful recruitment depends on the existence of sufficient areas containing such particles at proper densities and co-occurring with first-feeding anchovy larvae.

OBJECTIVES

To discover the extent, both horizontal and vertical, of larval anchovy feeding areas and how these change with time and a variety of oceanographic and meteorological conditions, a survey of inshore and offshore particle distributions was made off southern California from September 1974 through September 1975. This period spanned a complete anchovy spawning season which normally occurs from January to May (Fig. 183). The temporal and spatial picture of the anchovy larva's micro- and macro-environment was expected to suggest whether conditions were good for larval anchovy feeding and hence whether good or bad recruitment might be expected on the basis of larval food distribution.

Specifically, the following were measured: 1) the extent, persistence and patchiness of organisms causing chlorophyll maximum layers, 2) the relationship of these organisms to the distribution of first-feeding anchovy larvae, 3) the concentration of > 20 μm "effective diameter" particles and their size distribution, 4) the relationship of phyto- and microzooplankton patches to environmental conditions, e.g.,

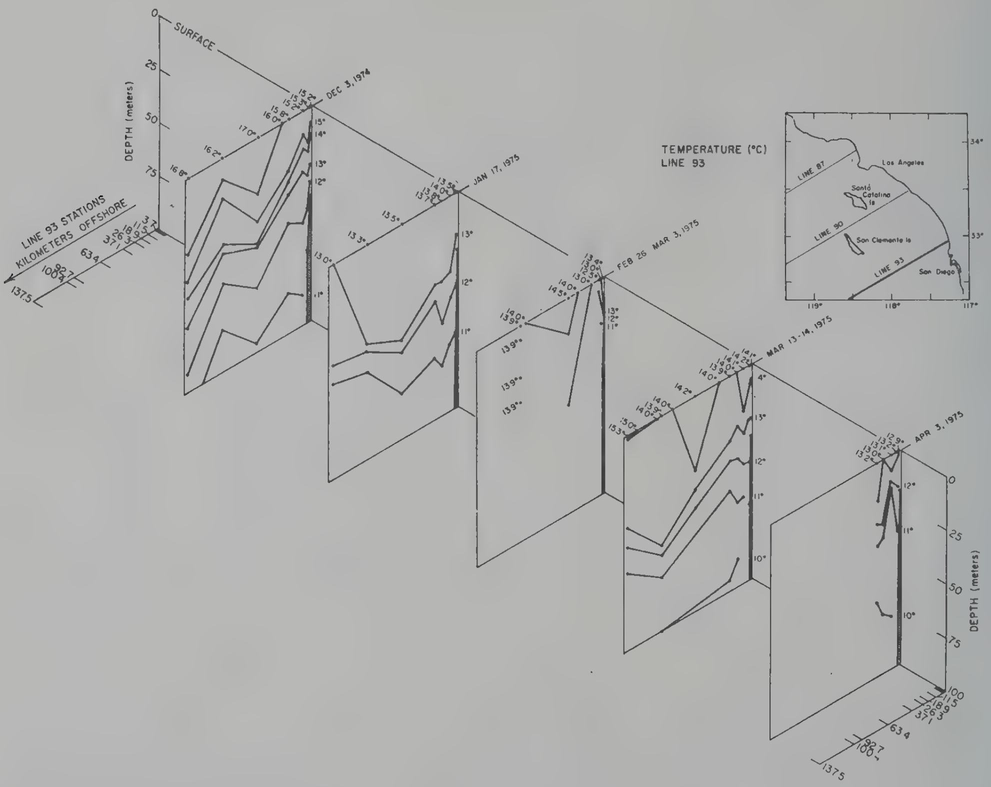

Figure 187. Temperature profiles during five cruises from November 1974 to April 1975. Line 93 extends from Del Mar, California to offshore.

storms and upwelling, and 5) the nutritional value of the dominant larval anchovy food organisms.

METHODS

An intensive sampling pattern in the inshore zone (Fig. 182) was established during the regular California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey using the RV "David Starr Jordan". This was done to determine the seaward extent of chlorophyll maximum layers shallower than 30 m. Thirty metres depth was chosen because Ahlstrom (1959) (data summarized by Hunter and Sanchez, 1976) showed that over 80% of northern anchovy larvae smaller than 12 mm long are found in water shallower than 30 m, while most yolk-sac and newly feeding larvae are nearer the surface. Cruises of the RV "David Starr Jordan" were held about monthly from September 1974 through September 1975.

A 3/4 h.p. – 110 V submersible centrifugal pump[2] was used with 30 m of 2·54 cm inside diameter flexible hose deployed over the ship's side to detect chlorophyll and particle concentrations. A stream of water was ducted to a Turner fluorometer onboard and the chlorophyll depth profile recorded. Samples of water (200 ml) were taken from just under the surface and from the chlorophyll maximum layer for particle

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[2] Prosser Industries, Inc., 900 E. Ball Road, Anaheim, California 92803 Pump No. 9-911-7.

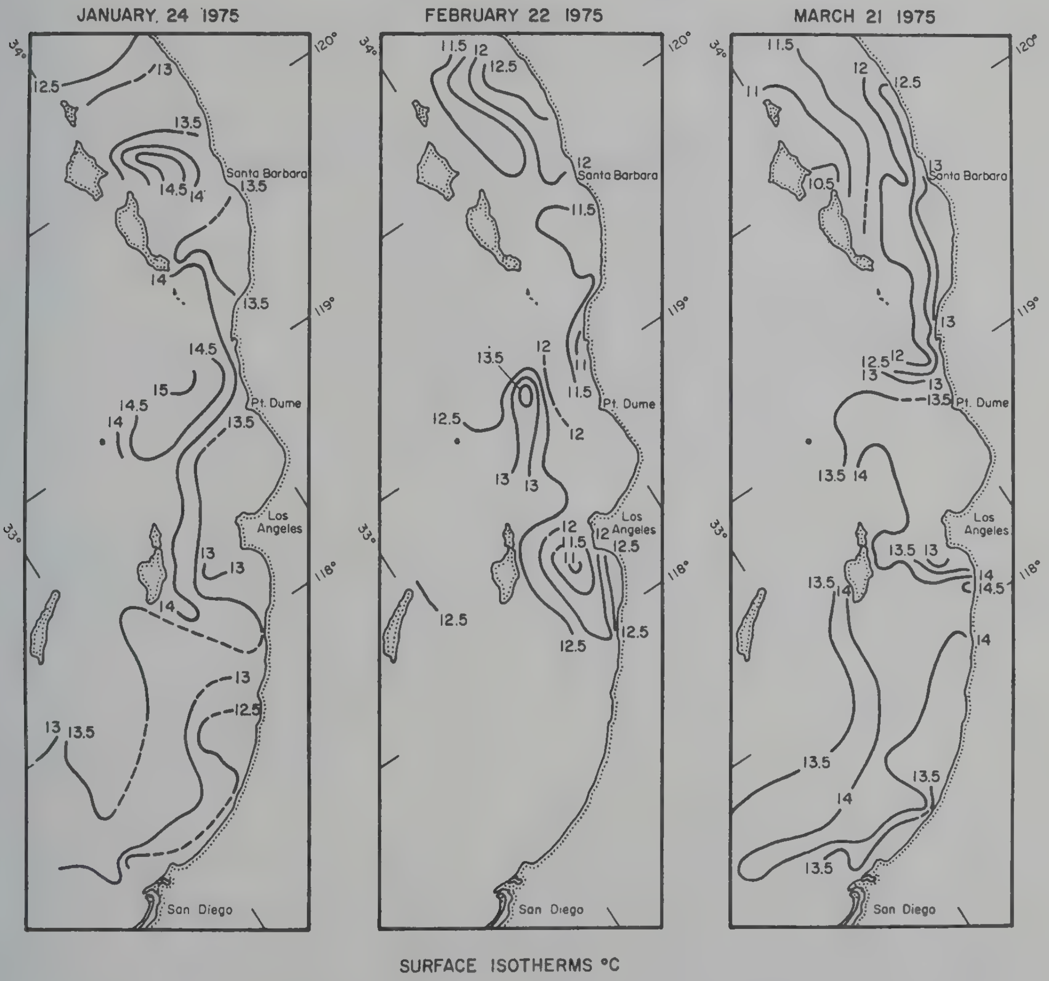
JANUARY 24 1975
FEBRUARY 22 1975
MARCH 21 1975
34°
33°
120°
119°
118°
Santa Barbara
Pt. Dume
Los Angeles
San Diego
12.5
13
13.5
14
14.5
15
11.5
12
11
10.5
SURFACE ISOTHERMS °C

Figure 188. Surface isotherms obtained by U.S. Coast Guard overflights with an infra-red radiometer.

counting and sizing with a 16-channel Model Ta Coulter Counter using a 280 μm pore and for determining the chlorophyll *a* component (Kiefer and Lasker, 1975). When no subsurface chlorophyll maximum was found, a water sample was taken routinely from 15 m depth. In each instance an additional 500 ml water sample was preserved with strontium-chloride-fortified-formalin as described by Beers and Stewart (1970) for later microscopic examination. No particles smaller than 20 μm effective diameter were counted with the Coulter Counter, but all particles having at least one dimension, 20 μm or longer, were identified and counted microscopically. The latter usually included most of the diatom species found in the Southern California Bight.

Anchovy larvae were collected in oblique plankton tows with a 1 m mouth diameter plankton net (mesh size, 0·505 mm). Larvae were sorted from other

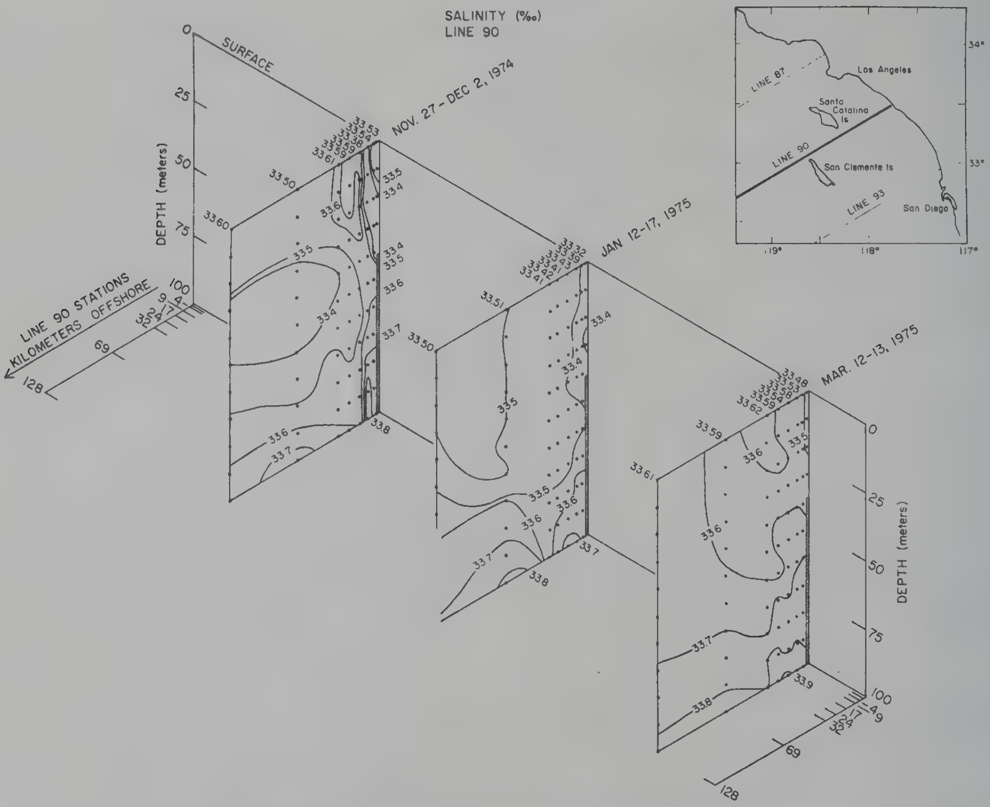

Figure 189. Isohalines along line 90, November 1974 to March 1975.

plankton, measured and counted. Details of these operations are given by Kramer et al (1972). Larval anchovy concentrations are given as numbers of larvae under 10 m^2 of sea surface.

Salinities and temperatures with depth were recorded at each station with a Plessey STD. In September 1974, February 1975 and June 1975, cruises by the Food Chain Research Group of the Scripps Institution of Oceanography occupied three regular CalCOFI transects and their information supplements that obtained by the RV "Jordan".

The CalCOFI basic station plan (Anon, 1963) shows the major stations occupied on every CalCOFI cruise. The three transects studied most intensively in this investigation were Lines 87, 90 and 93. The relative positions of these three transects are also shown in Figure 182.

OCEANOGRAPHY OF THE SOUTHERN CALIFORNIA BIGHT DURING THE 1974–1975 NORTHERN ANCHOVY SPAWNING SEASON

Annual spawning season

The distribution and aggregation of larval food, composed of microplankton > 30 µm effective diameter, is greatly affected by currents, turbulence, upwelling and downwelling. Therefore, oceanic conditions in the Southern California Bight were closely monitored during the 1974–1975 spawning of the

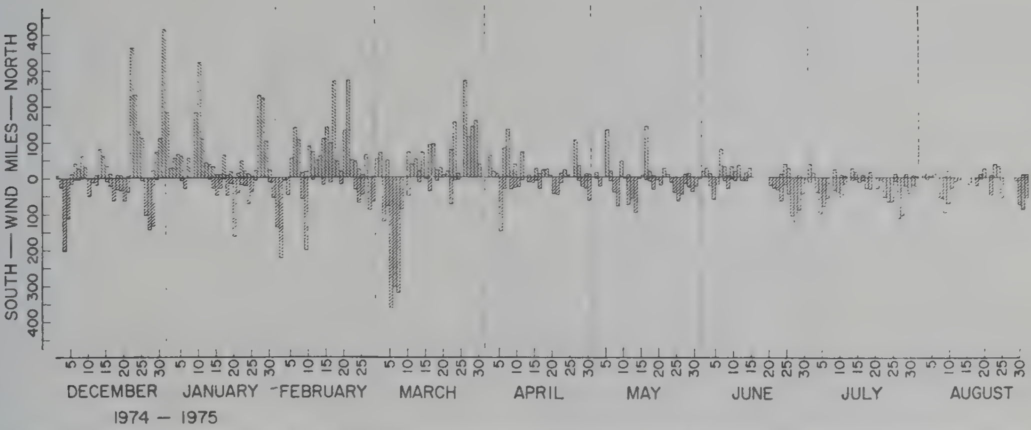

Figure 190. North and south wind miles at San Clemente Island. Wind miles were calculated by multiplying hours and wind speed. Major upwelling was noted on February 22 after about a week of northerly winds.

northern anchovy. Usually, spawning by the northern anchovy occurs over the winter and early spring months, but mostly during February, March and April (Fig. 183). This temporal spawning pattern was repeated in 1974–1975 (Fig. 184). The February–March 1975 spawning in the Southern California Bight was substantially greater than it had been in the previous five years (Smith, pers. comm.).

When plankton tows were made to sample anchovy larvae and their food, vertical profiles of water temperature and salinity were taken simultaneously. A weather station on San Clemente Island provided wind and storm data.

WATER TEMPERATURES OF THE SOUTHERN CALIFORNIA BIGHT

Stable water temperatures were characteristic of the Southern California Bight from September 1974 through early December 1974. For example, surface temperatures over the entire Bight were between 15°C and 17°C along the three major transects in the Bight, lines 87, 90 and 93 (Figs 185, 186 and 187) the first week of December. A sharp thermocline extended from the shore out to approximately 10 km and the entire length of the bight, about 300 km. Surface cooling was particularly evident when the 12–17 January cruise was held. A deep (25–50 m) mixed layer of 12° to 13°C developed along line 87, and at 13° to 14°C along lines 90 and 93. In February, 11°C was common inshore and was indicative of a major upwelling event (Fig. 188).

SALINITY STRUCTURE OF THE SOUTHERN CALIFORNIA BIGHT

Southern California Bight water was generally less saline in mid-January ($33{\cdot}3$–$33{\cdot}4^0/_{00}$ S) inshore than it was in early December ($33{\cdot}5$–$33{\cdot}6^0/_{00}$). No strong upwelling was evident. The hyposaline condition ($33{\cdot}3$–$33{\cdot}4^0/_{00}$) (Fig. 189) can be explained by a southward flow next to the coast, associated with a clockwise gyre typical of winter circulation in the southern part of the Bight (Jones, 1971).

UPWELLING

Strong upwelling began in February in the Bight after the onset of northerly winds (Fig. 190) and was clearly evident from the appearance of depressed temperatures (11°–12°C) inshore coincident with the appearance of diatoms (see following section).

A series of storms with strong southerly winds started on 3 March and lasted one week. The appearance of higher salinities inshore indicated a northerly flow of water and convergence (downwelling) throughout the Bight. After this stormy period, upwelling recommenced as shown by the generally colder water inshore and the upward thrust of the colder (11° and 12°C) isotherms in April (Figs 185, 186 and 187). Similar upwelled conditions prevailed through the following spring and summer months.

These data show that there was a typical winter circulation in the Southern California Bight. Generally calm conditions presaged the annual anchovy spawning cycle. January in particular was not stormy but

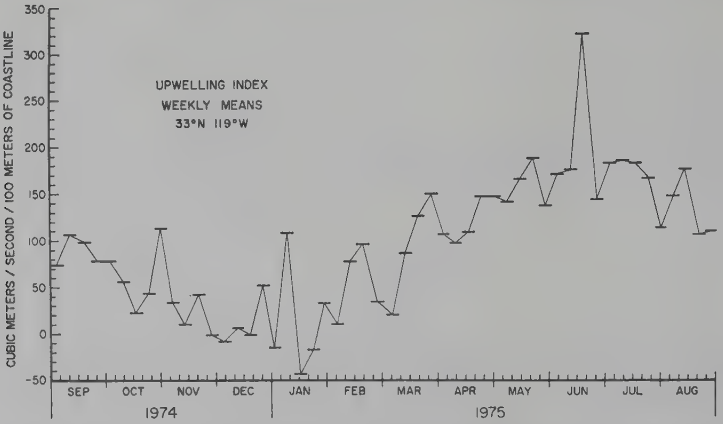

Figure 191. Upwelling index, September 1974–September 1975, calculated at San Clemente Island for the Southern California Bight. Upwelling is given as flow of water in $m^3 s^{-1} 100 m^{-1}$ of coastline (Bakun, 1975).

there was sufficient water circulation and surface cooling in the Bight to obliterate the thermocline and, as will be seen from the following section, to distribute potential larval fish food throughout the Bight. Northwest winds (Fig. 190) prior to the 26 February to 3 March sampling cruise presumably caused divergence of water from the inshore zone resulting in a significant upwelling which was reversed in the days that followed. This alternation of upwelling and relaxation over a 2-week period was associated with a thorough mixing of the upper isothermal (13°–14°C) layer. Two weeks later, in early April, upwelling was firmly established once more and continued throughout the rest of the spring and summer. This alternation of upwelling and relaxation, as shown by temperature profiles, is also reflected by Bakun's (1975) upwelling index for the 3° square encompassing the Southern California Bight and measured at 33°2′N 118°36′W, at the northern tip of San Clemente Island, 55 m elevation (Fig. 191). Infra-red satellite photographs of the Southern California Bight and Baja California showed that upwelling had commenced at least as early as 21 February 1975 and extended as far south as Vizcaino Bay at that time, 723 km from Los Angeles, California. This encompassed virtually the entire larval anchovy's feeding grounds.

POTENTIAL LARVAL ANCHOVY FOOD PARTICLES IN THE SOUTHERN CALIFORNIA BIGHT, 1974–1975

In March 1974, at the height of the 1973–1974 anchovy spawning season, the unarmoured dinoflagellate *Gymnodinium splendens* (30–50 µm effective diameter) was the dominant organism inhabiting inshore chlorophyll maximum layers (Lasker, 1975). By September 1974, in the same inshore areas, the common red tide organism, the armoured dinoflagellate *Gonyaulax polyedra* dominated the chlorophyll maximum layers. *G. splendens* was no longer seen. The areal extent and temporal persistence of *G. polyedra* was striking; an apparently continuous layer about 300 km long, and 5 km wide, extended from at least Point Conception to San Diego ranging in concentration from 20 to 2000 cells/ml in the chlorophyll maximum until January 1975 when *G. polyedra* in relatively high concentrations was distributed throughout the Southern California Bight. Table 14 and Addendum summarize phytoplankton and microzooplankton species and relative densities along line 90 from September 1974 through July 1975. The spatial and temporal distribution of dinoflagellates and diatoms is shown graphically in Figure 192.

From September 1974 until early February 1975, *G. polyedra* was the numerically abundant organism in the size range eaten most often by first-feeding anchovy larvae. The high number of particles displayed do not occur throughout the water column, but rather appear either at the surface or in well-defined chlorophyll maximum layers, most 15–20 m below the surface. In January (Fig. 193), *G. polyedra* was no longer confined to within a few kilometres of the shore, but was prevalent in high concentrations, i.e., > 35 cells/ml, throughout the Bight, presumably distributed by the usual winter gyral movement of

Table 14. Species composition and relative numerical abundance of phytoplankton and microzooplankton along line 90 from September 1974 through September 1975. All stations were within 9·5 km. Stations and depths selected for this table had the highest overall concentrations of organisms. Note the disappearance of *Gonyaulax polyedra* and the appearance of diatoms after the early February sampling, presumably as a result of a major upwelling event.

Key; Cells/ml: 0·1–0·9 (+); 1–9 (++); 10–99 (+++); 100–999 (++++).

DATE DISTANCE FROM SHORE (KM) AND DEPTH (M)	DINOFLAGELLATES												DIATOMS																									
	Gonyaulax polyedra	Ceratium furca	Ceratium fusus	Dinophysis caudata	Peridinium spp.	Prorocentrum micans	Ceratium spp.	Dinophysis spp.	Gymnodinium spp.	Misc. Unarmored Dinoflagellates	Misc. Armored Dinoflagellates	Oxytoxum spp.	Nitzschia spp.	Rhizosolenia spp.	Biddulphia sp.	Chaetoceros spp.	Thalassiothrix frauenfeldii	Unidentified Chain Diatoms	Asterionella japonica	Thalassiosira spp.	Skeletonema costatum	Eucampia zoodiacus	Coscinodiscus spp.	Ditylum brightwelli	Thalassionema nitzschioides	Misc. Diatoms (> 20 µ)	Unidentified Cells (20-50 µm)	Unidentified Cells (50-100 µm)	Silicoflagellates	Coccolithophores	Ciliates	Tintinnids	Holotrichs	Copepod nauplii	Radiolarians & Foraminiferans	Unidentified particles (20-50 µm)	Unidentified particles (50-100 µm)	Unidentified particles (>100 µm)
Sept. 13-20, '74 0.93 km (3m)	+++	++	+	++	++	++	++																			++	++	+				+	++		++	+++	++	
Nov 26-Dec. 19 '74 1.85 km (13.5m)	++++		++	++	++		++					++		++													+++	++		++			++			++	++	
Jan. 12-Feb. 3 '75 9.45 km (14m)	++++	++			++		++				++		+++	++	++	++	++									++	++	++		++	+				+	+++	++	++
Feb. 26-Mar. 3 '75 0.93 km (1m)	++	++			++		+		++	++++			++++	++		+++	++	++		++	+++					++	++	++	++		+	+	+			++	++	++
Mar. 6-26, '75 1.85 km (30m)								+		+			+++	++		++	+++	++			+	++	+			++	++	++	+	+	++	+	++	+		+++	++	+++
Apr. 1-3, '75 1.85 km (17.5m)										++			+++	+++	++	++++	++++		+++	++++	+++	++		+++	+++	+++	++									+++	+++	++
May 15-26, '75 4.08 km (15m)					+		+			+	+			+	+											+	+	+	+		++	++	++	+		+++	++	++
June 16-24, '75 0.93 km (12 m)		++			++	++	+	++	++	++		+	+++	++	++	+++		+++								+	++	+			+	++	+	+		++	++	++
June 24-July 7, '75 4.08 km (10 m)	++	+			+	+++	++	++		++		+	+++	++	++	++		++	++		+	++++				++	++	+			+	++	+		+	++	++	++
Sept. 6-14, '75 0.93 km (Surface)	++	++	++		++	++	++	+	++	++	++	++															++	+	+		++		+	+		+++	++	++
Sept. 13-22, '75 1.85 km (22 m)								+						+													+								+	++	++	+

water[3] (Schwartzlose, 1963) and favourable conditions for reproduction. First-feeding anchovy larvae appeared in the Bight in January. Twenty-five first-feeding larvae of 253 examined in that month had discrete particles in their intestines; sixteen of the twenty-five contained *Gonyaulax*.[4] Five weeks later, as a result of an upwelling which encompassed the entire Bight, the number of particles with effective diameters of 30 µm and larger over the entire area was reduced

[3] Advection of southerly water cannot be dismissed as a possibility.

[4] While particle size and density are limiting characteristics for larval anchovy survival, the nutritive value of the food particles may also be an important factor. A number of feeding experiments with laboratory cultured *G. polyedra* and laboratory hatched *E. mordax* larvae showed that first-feeding larvae did not grow well on *G. polyedra* as a sole diet, whereas they can on the unarmoured dinoflagellate *Gymnodinium splendens* (Scura and Jerde, 1977). A dominant, but nutritionally inadequate, food for anchovy larvae provides an additional cause for unfavourable survival of an anchovy year class.

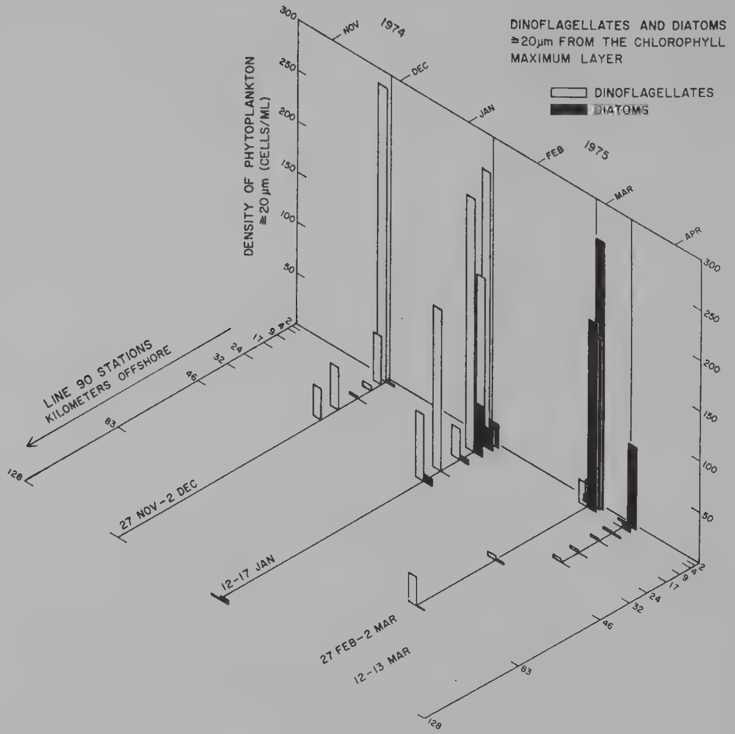

Figure 192. A comparison of diatom and dinoflagellate abundance along line 90 over the anchovy spawning season.

far below that necessary for first feeding and survival by anchovy larvae. This is shown graphically in Figure 194.

The importance of this event and its possible effect on survival of fish larvae should be emphasized. Chlorophyll *a* measurements (Fig. 195) and the replacement of dinoflagellates by diatoms show clearly the response to the major upwelling in the Bight during February and March 1975. However, my own laboratory and field results, and the work of Arthur (1976) and Berner (1959) show that anchovy larvae have a particle size threshold for feeding; small diatoms, whether in chains or as single cells and regardless of concentrations are usually not large enough to be seen or are ignored for other reasons by first-feeding anchovy larvae.

Thus, despite the obvious benefit to phytoplankton production that upwelling brings to coastal waters, the disruption of well-defined layers and aggregations of suitable larval fish food organisms is undoubtedly detrimental to the larvae relying on such aggregations. In other words, those oceanographic features which favour stability in inshore waters can be classified as favourable for anchovy larval fish feeding, while those which cause instability should be considered to be detrimental to larval survival. Nelson et al (1976) showed in a different environmental context that menhaden larvae which depend on nursery grounds in estuaries for food are carried into the estuaries during downwelling periods. In this instance, upwelling also acts to the detriment of larval survival but by a different mechanism.

Hunter (in press) has shown that northern anchovy larvae can exist and grow until they are 6 mm in length on particles approximately 40 µm in diameter, e.g., *Gymnodinium*. The larvae remain 6 mm in length as long as there are 40 µm particles in high enough concentrations on which they can subsist. It is im-

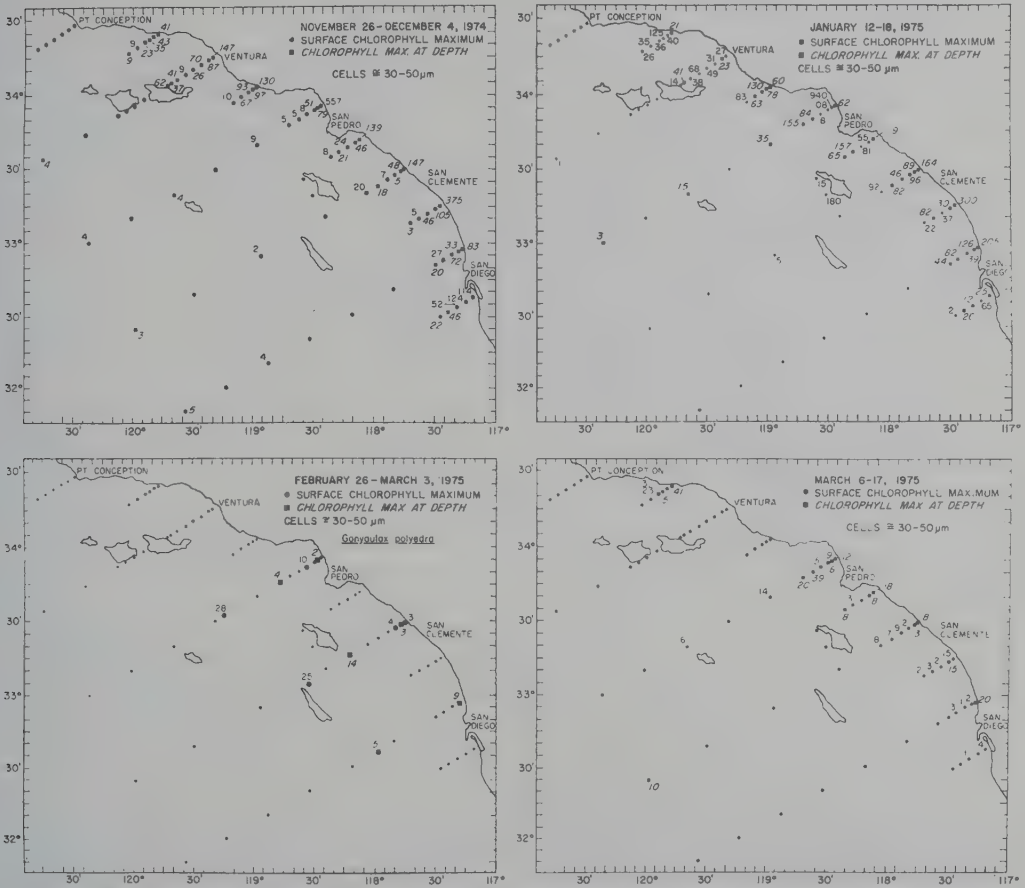
NOVEMBER 26–DECEMBER 4, 1974
● SURFACE CHLOROPHYLL MAXIMUM
■ CHLOROPHYLL MAX. AT DEPTH
CELLS ≅ 30–50 μm
JANUARY 12–18, 1975
● SURFACE CHLOROPHYLL MAXIMUM
■ CHLOROPHYLL MAX. AT DEPTH
CELLS ≅ 30–50 μm
FEBRUARY 26–MARCH 3, 1975
● SURFACE CHLOROPHYLL MAXIMUM
■ CHLOROPHYLL MAX AT DEPTH
CELLS ≅ 30–50 μm
Gonyaulax polyedra
MARCH 6–17, 1975
● SURFACE CHLOROPHYLL MAXIMUM
■ CHLOROPHYLL MAX AT DEPTH
CELLS ≅ 30–50 μm
PT CONCEPTION
VENTURA
SAN PEDRO
SAN CLEMENTE
SAN DIEGO
30'
34°
33°
32°
120°
119°
118°
117°

Figure 193. The distribution of maximum counts of 30–50 μm particles in the Southern California Bight from November 26 1974 to March 17 1975. Note the inshore prevalence of these particles in late November and their widespread distribution in January.

possible for them, because of physical limitations, to capture enough of these small particles once they have attained this size to do any more than maintain their metabolic requirement. However, should larger particles become available to them, enabling them to grow larger than 6 mm, this larger size precludes an ability to resort solely to small particles once again and the larva becomes locked into eating larger particles to meet its metabolic requirements. The implications of this are profound, i.e. from 6 mm on, anchovy larvae must encounter relatively high densities of larger particles to ensure their survival, yet these densities have not often been found in the sea. In other words, high densities of microzooplankters larger than 50 μm in diameter must exist, but are not reported in the literature.

Counts of micronauplii were made for samples taken along line 90 with a plankton pump to see if minimum numbers, as calculated by Vlymen (1977), would be found during the spawning season of the anchovy. Concentrations of nauplii as high as this were encountered rarely. For example, only two inshore water samples taken from the chlorophyll maximum layer, 0·9 km apart, showed 280 and 117 micro-

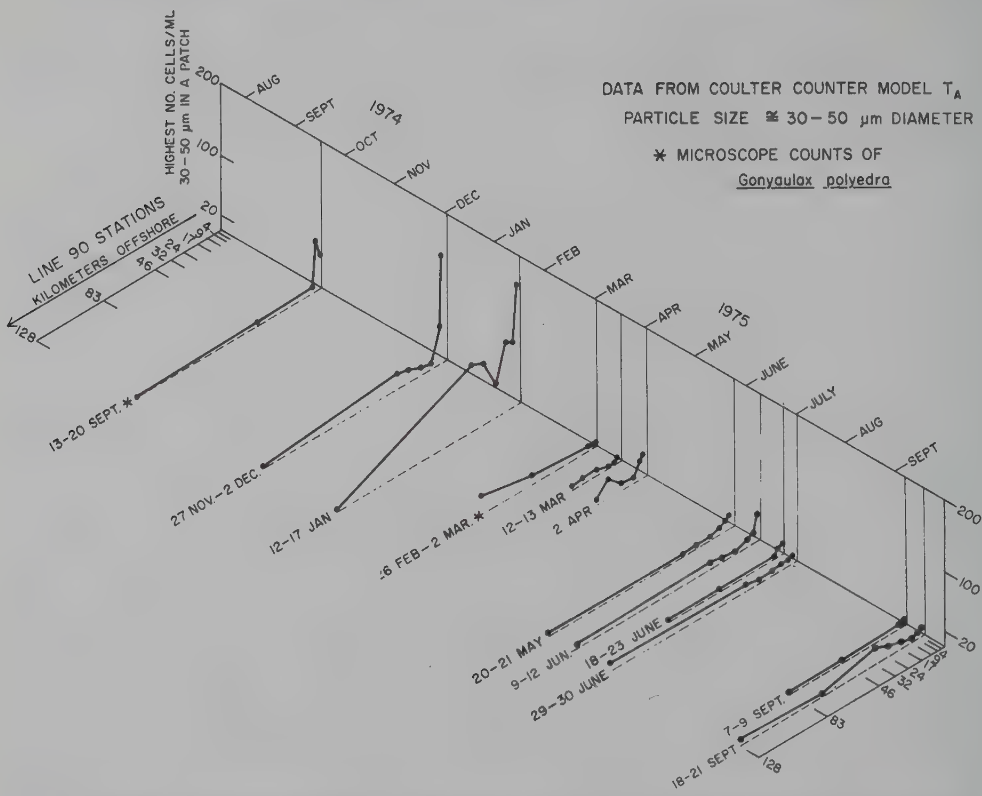

Figure 194. Spatial and temporal distribution of the highest number of 30–50 μm diameter particles found in the water columns throughout the Southern California Bight from September 1974 through September 1975. Note the high inshore particle concentrations in December and January.

zooplankters per litre, respectively. Both samples had the same size frequency distribution of organisms which included nauplii, copepod, post-nauplii and polychaete larvae. Nauplii were present in the greatest number in each sample (Fig. 196). Upwelling regions, as described in this paper, when they stimulate reproductive activity in copepods and other small plankters provide the necessary forage for anchovy larvae larger than 6 mm in length. If a larva grows to a larger size despite a dilution of its initial food during the upwelling process, the chances for survival may increase if regions of high naupliar and other microzooplankton densities are established in the wake of an upwelling event.

Throughout this study, concentrations of phytoplankton and zooplankton have been reported as they were taken with a plankton pump, which undoubtedly reduces concentrations of organisms at the opening of the pump and as water travels through the pipe to the shipboard laboratory. Thus, the key to defining microstratification, clumping and patchiness is the solution of a sampling problem for the particles which serve as food for fish larvae. Without doubt, there will be many areas found in the larval anchovy spawning ground which emulate the highest concentrations of organisms we have sampled with the techniques at hand. The spatial distribution and temporal persistence of high larval food concentrations is an important

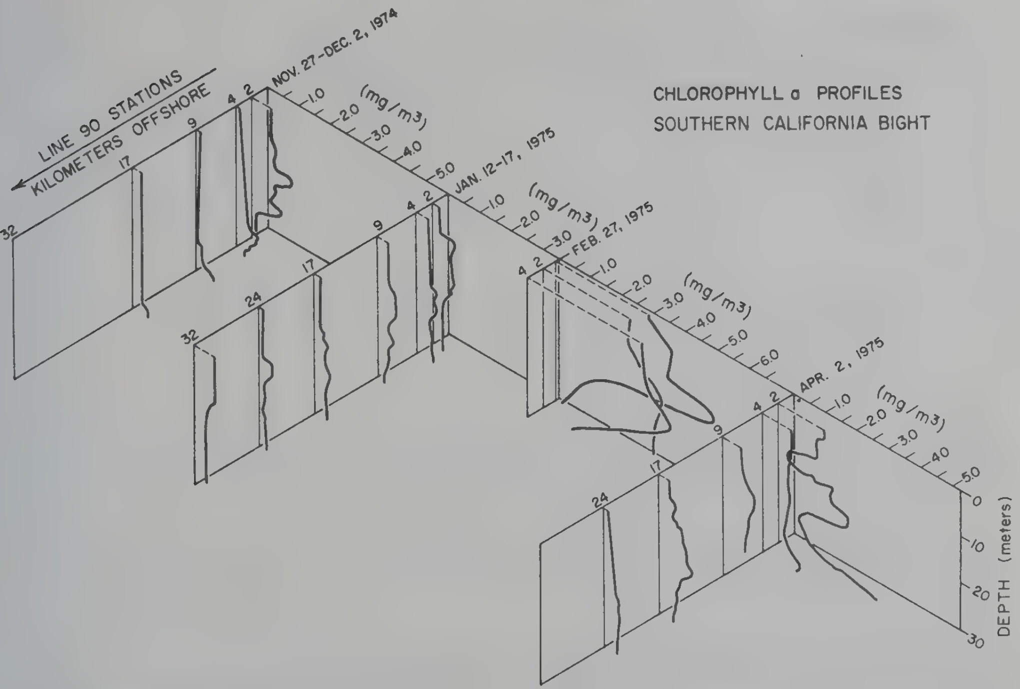

Figure 195. Chlorophyll *a* profiles for line 90 from November 1974 through early April 1975. High chlorophyll *a* in February is due to a diatom bloom (see Table 14).

area of study for elucidating the stock and recruitment relationship.

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SUMMARY

1) Northern anchovy larvae require at first feeding, relatively high densities of 30–50 µm particles for metabolism and growth. During the 1975 anchovy spawning season, dinoflagellates met these conditions in the main inshore spawning area of the anchovy off California.

2) Stable oceanographic conditions which foster stratification are needed to maintain high densities of dinoflagellates.

3) When particle sizes and concentrations were monitored over a complete anchovy spawning season in the Southern California Bight, it was seen that upwelling and storms could disrupt dinoflagellate layers. In February 1975, a massive upwelling throughout the Southern California Bight diluted dinoflagellate concentrations far below that needed by first-feeding anchovy larvae for metabolism and growth.

4) Despite the obvious value of upwelling to total algal productivity the diatoms which are first produced in numbers are too small or unacceptable behaviourally as food for first-feeding anchovy larvae.

5) Anchovy larvae can sustain themselves and grow to 6 mm on small particles. Once this size is attained further growth depends on large particles being eaten. Once larger particles are eaten the larva cannot rely on small particles any longer but must continue to seek and find large ones to maintain its metabolism.

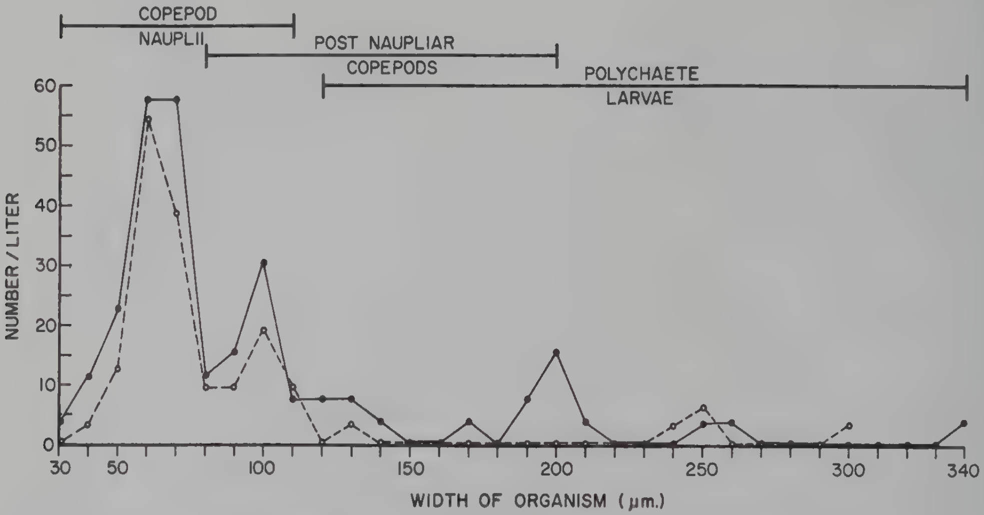

Figure 196. Width frequency distribution of two samples of microzooplankton taken in March 1976, 0·8 km apart within 2 km of the shore. Closed circles indicate the sample taken nearest the shore.

6) Microzooplankters are generally larger than 40 µm in width but were rarely found in high enough concentration to serve as food for larger anchovy larvae.

7) The most dominant dinoflagellate present during the 1975 anchovy spawning season was found to be nutritionally deficient in laboratory experiments.

8) The presence of a nutritionally inadequate dominant food as well as a massive upwelling in the midst of the anchovy spawning season suggests inadequate feeding conditions for the 1975 year class of anchovy during larval development. If this hypothesis is correct, the 1975 year class of the northern anchovy will be a relatively poor one.

ADDENDUM

A RÉSUMÉ OF PHYTOPLANKTON DISTRIBUTION FROM SEPTEMBER 1974 THROUGH SEPTEMBER 1975

September 1974

In the cruise period 13–20 September 1974, microscope counts revealed that *Gonyaulax polyedra* was the dominant species of phytoplankton in the Southern California Bight, with the highest density (about 2000/ml) in Santa Monica Bay (line 87), 67/ml off Dana Point (line 90) and 20/ml off Del Mar (line 93). *G. polyedra* was concentrated in the inshore zone along line 87, within 5–6 km offshore and within 3·7 km for lines 90 and 93.

Other organisms common in the Bight at the same time were the dinoflagellates *Ceratium furca* and *Prorocentrum micans*. *C. furca* averaged 10/ml on line 87 with a maximum of 27/ml. Lines 90 and 93 never had more than 2/ml of *C. furca* in September 1974. *Prorocentrum micans* averaged ≤ 5/ml for lines 87, 90 and 93. The maximum *P. micans* for line 87 was ~ 15/ml; ~ 10/ml for line 90 and ~ 6/ml for line 93.

Diatoms larger than 20 µm in effective diameter were not found at every station. Assorted diatom species were occasionally found in low concentrations (≤ 2/ml) along lines 87, 90 and 93. Highest densities were found on line 90, 1 km offshore with a maximum of 7/ml and 1·9 km offshore on line 93 with a maximum of 15/ml.

The density of *G. polyedra* in Santa Monica Bay was high enough to be seen as a red tide, 1 and 2 km offshore, with chlorophyll *a* concentrations of 27 and 36 mg/m^3 respectively. There was an average chlorophyll *a* content of 0·73 mg/m^3 along lines 90 and 93.

October 1974

On a special 1-day cruise 1 month later on 17 October 1974 off Dana Point (line 90), plankton pump samples were taken only from the inshore zone within a boundary extending 9 km offshore to delineate the seaward extent of the *G. polyedra* aggregations. *G. polyedra* was still the dominant species with *C. furca* second in number as it had been the previous month near line 90. *Gonyaulax* was concentrated within the first 7·4 km from shore, with a maximum number of 57/ml. However, it dropped off quickly in number at about 8·3 km offshore. *Ceratium furca* was also concentrated within the first 7·4 km offshore with a maximum of 29/ml dropping off sharply at 8·3 km to $\leq$ 2/ml.

Diatoms larger than 20 μm effective diameter remained sparse ($\leq$ 2·5/ml), except for two inshore stations which had densities of 20/ml and 6/ml, half of which were species of *Nitzschia*.

November–December 1974

A month later, sampling from 26 November to 19 December 1974 showed that *Gonyaulax polyedra* remained the dominant species in the Southern California Bight. The number of *G. polyedra* was uniformly high at all the inshore stations, with densities of around 100/ml. Santa Monica Bay (line 87) again had the highest concentrations (870/ml).

C. furca continued to be found in small numbers, $\leq$ 5/ml over the entire Bight. No other dinoflagellates were in notably high concentrations.

Diatoms were, on the average, less than 1% of the number of dinoflagellates in the same size range along lines 83 (off Ventura, California) and 90, while line 87 had 8% diatoms to dinoflagellates.

The average chlorophyll *a* content for each line was $\leq$ 1 mg/m^3, with the exception of line 87, which averaged 1·63 mg/m^3. The maximum chlorophyll *a* for each transect was less than 4·0 mg/m^3, again with the exception of line 87, which had a maximum of 10·37 mg/m^3. As indicated in the previous section describing the oceanography of the Southern California Bight, no turbulent conditions were prevalent which could have disrupted the dinoflagellate concentrations.

January–February 1975

In the following month during 12 January to 3 February 1975, *G. polyedra* was not only found in high concentrations ($\sim$ 100/ml) at the inshore stations, but occurred as far as 25 km offshore along lines 87 and 90, in relatively high numbers (see Fig. 193).

Diatoms[5] increased moderately in number in the entire Bight averaging 55/ml in chlorophyll maximum layers on line 81·5, 46/ml along line 87, and 17/ml along line 90. Diatoms became fewer in number beyond Station 90·30 (17 km from shore).

The average chlorophyll *a* content throughout the Southern California Bight was higher than in December. Transects north of Dana Point had an average of about 2 mg/m^3 chlorophyll *a* and < 1·5 mg/m^3 south of Dana Point. The maximum chlorophyll content, depending on the transect, varied from 1·5 to 4·3 mg/m^3 (Fig. 195).

Water circulation in January favoured the horizontal distribution of *G. polyedra* throughout the Southern California Bight resulting in a large increase in areal distribution of this potential larval fish-food organism.

26 February–3 March 1975

By the sampling period 26 February to 3 March, there had been a sharp decline in the *G. polyedra* populations. Less than 10/ml were found within 18·5 km off the shore along lines 87, 90 and 93, while in general cell numbers above 25 cells/ml were only found far offshore (46 km) (Fig. 193).

Diatoms were higher in number than in January and were concentrated in the inshore zone. Various species of *Nitzschia* were most abundant in the Bight: *N. pacifica*, *delicatissima*, *pugens* and others. Species of *Chaetoceros* were also common at stations where diatoms were > 80/ml, while the number of dinoflagellates was less than one quarter the number of diatoms. Line 90 had about 200 diatom cells or chains within 4 km offshore, while line 93 had 52 cells or chains per millilitre about 2 km offshore. This was the result of the strong upwelling period during February (see section on oceanography) characterized by cold water close inshore.

The chlorophyll *a* content became significantly higher inshore. The average chlorophyll *a* for lines 87, 90 and 93 were from 3 to 5·5 mg/m^3. Line 87 had the highest maximum value of 15 mg/m^3 about 2 km offshore. Lines 90 and 93 had the highest maximum value of 15 mg/m^3 about 2 km offshore, and maxima of 5 and 8 mg/m^3 respectively within 2 km offshore (see Fig. 195).

6–26 March 1975

The 6 March to 26 March cruise period was the height of the northern anchovy spawning season (see following section). However, *G. polyedra* continued to diminish in number during March and reached a low concentration of 3/ml along line 90. This was characteristic of dinoflagellate concentrations throughout the entire Bight.

The diatoms *Chaetoceros* and *Nitzschia* species remained common although in lower number than in the previous weeks. Along line 90, the diatom concentration peaked at 2 km offshore at 81 cells or chains per millilitre dropping to an average of 2/ml for the next 23·7 km offshore. The diatom populations on each sampled transect showed similar species composition and numbers (Table 14).

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[5] Species of *Chaetoceros* and *Nitzschia* were the most common diatoms over the whole Bight. With respect to chain diatoms, each cell was counted microscopically as a single organism in those species whose single cell size was $\geq$ 20 μm in any dimension. Species with cells < 20 μm long were counted by chains. For example, because *Chaetoceros* cells are less than 20 μm long, the concentration per millilitre reflects the number of *Chaetoceros* chains, not individual cells in each chain.

1–3 April 1975

In early April, *G. polyedra* had virtually disappeared from the Southern California Bight and the entire region was dominated by diatoms. The number of diatoms increased from March in the inshore zone. On line 87, a station ~2 km offshore had a count of 76 diatoms/ml with a great deal of detritus < 20 μm in diameter in the water. At ~3·5 km offshore, diatoms increased to 858/ml. On line 88·5 at a station ~5 km offshore, the density of diatoms was 480/ml increasing to > 1000/ml about 8 to 9·5 km offshore. Line 90 had diatoms > 1000/ml 2 km offshore with small detritus 10–30 μm. Diatoms dropped to ~300/ml, 4 km offshore and then to < 271/ml from 9–32 km offshore. Line 95 had over 3600 diatoms/ml within 3·7 km offshore. About 3500/ml of these diatoms were a chain diatom identified as a species of *Leptocylindricus* (diameter 4–7 μ). Species of *Chaetoceros* and *Thalassiothrix frauenfeldii* were the most common and abundant species of the Bight, with the exception of *Leptocylindricus* which was found in dense concentrations only along line 93. Of the total number of cells with diameters from 16·0 to 161 μm, the majority of cells (40–60%) fell in the 16–20 μm size range for lines 87, 90 and 93. Cells with effective diameters of 30–50 μm, i.e. the size required by anchovy larvae at first feeding were frequently high, i.e. > 30 particles/ml in the Bight; but these were due to diatom chains and are not eaten by anchovy larvae (Lasker, 1975).

Dinoflagellates were less than 2% the number of diatoms at each station along lines 87, 88·5, 90 and 93 except for those at which the numbers of diatoms dropped to ≤ 27/ml. At these stations, both diatoms and dinoflagellates were similarly low in density.

The average chlorophyll *a* content in the beginning of April was ~25% lower than the February–March cruises for line 90 with 2·4 mg/m³ and line 93 with 3·8 mg/m³. Maximum chlorophyll values for lines 90 and 93 were ~8 and 6 mg/m³, respectively. Line 87 decreased also from an average of ~5·5 mg/m³ in February–March to ~2 mg/m³ in April. From line 88·5 through 91·5, the average chlorophyll was around 2–5 mg/m³ with a maximum of 7–8 mg/m³.

15–26 May 1975

Not a single *G. polyedra* was identified along line 90 during the May cruise.

Particle counts for 30–50 μm particles were even lower than during the April 1975 cruise. For example, along line 87 there was an average of 7/ml to 25 km offshore. Line 90 averaged only 17/ml within 4 km offshore. Line 93 had particle counts averaging 10/ml within 26 km offshore.

The diatom "bloom" of early April had dissipated by mid-May. On line 90, diatoms were 18/ml 2 km offshore. Further offshore the number of diatoms dropped to < 3/ml to as far as 32 km offshore.

Dinoflagellate concentrations were very low, < 7/ml, averaging < 2/ml for line 90. Not one species of dinoflagellates was especially common; mostly miscellaneous unarmoured dinoflagellates were present.

The average chlorophyll *a* content for the Bight was < 1·5 mg/m³ during this period.

16 June–5 July 1975

Between 16 and 24 June particle counts for 30–50 μm particles were ≤ 40/ml for lines 87, 90 and 93 with the exception of a station on line 87, about 1 km offshore which had 129/ml. Microscope counts of water from this station showed a large number of armoured dinoflagellates: *Ceratium dens*, *C. furca*, *Dinophysis* sp. and *Peridinium* sp.

On lines 90 and 93, dinoflagellates numbered, on the average, 3·5/ml with a maximum inshore of 12/ml. Species of *Prorocentrum*, *Ceratium*, *Gymnodinium*, and *Peridinium* were identified.

Within 2 km offshore there was an average of 44 diatoms/ml. At 46 and 83 km, diatoms averaged in number about 90/ml. Chain diatoms, *Chaetoceros* and *Nitzschia*, comprised the inshore diatoms. Farther offshore (46–83 km), *Nitzschia* was most numerous.

The chlorophyll *a* content had increased since the mid-May cruise. Line 87 had an average of ~5 mg/m³; line 90, an average of 3 mg/m³. Line 93 remained about the same with an average of 2 mg/m³.

The particle counts, species identification and chlorophyll *a* measurements were repeated for the entire Bight from 24 June through 7 July 1975. No major differences were seen in any of the measurement parameters.

6–22 September 1975

No cruises were held during late July or August. In September, low numbers of 30–50 μm particles prevailed. Very low dinoflagellate counts were characteristic.

20 October–2 November 1975

Repeating the pattern of the previous year, a dinoflagellate bloom was evident in October. All along the coast from line 83 down to line 95, microscope counts revealed *Gymnodinium uberrimum* (40–

60 µm) to be the dominant organism. *G. uberrimum* numbered 40–50/ml along line 90 within 4 km offshore and was present in lesser concentrations (2–4/ml) out to 32 km offshore. Line 95 had 64/ml 4 km offshore. At a nearshore station on line 83, the density of *G. uberrimum* was 1363/ml.

Diatoms were slightly higher than during the 13–22 September cruise, especially in the inshore zone. Line 90 had a maximum of 15/ml. Line 83 had 28/ml. *Nitzschia* was the most common species.

There appeared to be an unusually high number of coccolithophores along line 90 from 9 km to 17 km offshore. The density of these organisms was 15–19/ml. In past cruises, coccolithophores did not number more than ~5/ml.

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GROWTH AND SURVIVAL OF FIRST-FEEDING NORTHERN ANCHOVY LARVAE (*ENGRAULIS MORDAX*) IN PATCHES CONTAINING DIFFERENT PROPORTIONS OF LARGE AND SMALL PREY

Reuben Lasker and James R. Zweifel

National Marine Fisheries Service, NOAA
Southwest Fisheries Center
La Jolla, California 92038

INTRODUCTION

As early as 1914, Hjort proposed that differential mortality of first-feeding larvae due to variable feeding conditions could be the cause of extreme variations in year class strength of fish. Tests of this simple attractive hypothesis have given equivocal results at best. With regard to clupeid larvae, on the average, there is usually not enough food available for the larvae to survive, considering the amount of water a larva is capable of searching and its inefficiency in capturing food when it first starts to feed (Hunter, 1972). With the sampling gear currently used (pumps and plankton nets*), it is still difficult to establish whether any body of water can support enough larval fish survival to ensure the establishment of a robust year class. To do so, however, would be a first step toward defining criteria for successful recruitment, a recognized need in all fisheries research today (Gulland and Boerema, 1973). The success of pelagic fish in their environment has prompted fishery scientists to postulate that there have to be suitable concentrations of food organisms in space and time (patches) to provide for larval feeding and that Hjort's hypothesis is still viable and should be rigorously tested.

The significance of food aggregations for larval fish can only be assessed if we know important features of larval feeding behavior. Although we know relatively little about the behavior of most fish larvae, it is possible now, with at least one species, *Engraulis mordax*, to assemble the pertinent behavioral data as a result of some recent intensive laboratory and field investigations. Two recent papers by Lasker (1975 and 1978) have provided evidence for the aggregation of properly sized food particles in the habitat of the first-feeding larval anchovy off California. He found that stability of the water column in the upper 30 meters appeared to be the key condition required for larval anchovy food organisms to aggregate in densities high enough to exceed the threshold for the feeding stimulus of first-feeding Northern anchovy larvae. Disruption of this stability was caused by vigorous storms or by upwelling along the coast, both resulting in a dilution of the microplankton needed for feeding and, by inference, excessive mortality of any larvae which needed to feed immediately after these events occurred. In addition, the work of Hunter (1972, 1976, 1977), Hunter and Sanchez (1976), Arthur (1976, 1978), Lasker (1964), Lasker *et al.* (1970) and Vlymen (1974, 1977) provide us with a background of behavioral and physiological information on the larvae of the northern anchovy, *Engraulis mordax*. The interest in anchovies goes beyond their importance in the California Current ecosystem; anchovies contribute to some of our largest fisheries, and, indeed, when the Peruvian anchovy fishery was at its peak, the anchovy catch made up 25% of the entire world fish catch.

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*Both kinds of gear sample a lot of water and tend to give results which average numbers of organisms over depths or distances and consequently obscure fine-scale patchiness of larval fish food.

These studies suggest that patchiness, which results in relatively high concentrations of larval anchovy food, is a major factor in the survival of clupeid larvae, although, as we will illustrate, high concentrations alone cannot be the sole criterion for survival. Other factors, such as the nutritive value and digestibility of the food, size of the food particle, food selection by the larva, learning by the larva, and a variety of other behavioral modalities, have to be taken into consideration if one is to predict whether a particular feeding regime will be favorable to larval anchovies. In this investigation, we consider the naive*, first-feeding anchovy larva presented with food on the first day it is capable of feeding. Patchiness obviously provides higher absolute concentrations of food particles than is usually found in the anchovy larva's environment. We attempt to show here that high food concentrations characteristic of patches in the sea, which appear to provide abundant food in the normal foraging distance of the larva, may still not be sufficient to provide for larval anchovy growth and survival on the first day of feeding. Because of the rapid development of learning in larvae and the increase in success of capture and selectivity, we have chosen to analyze only the first day of feeding by anchovy where learning has not had the opportunity to develop. However, we believe this modeling technique can be extended to assess growth and survival in older larvae as well.

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*The term naive encompasses both the concept of non-selectivity of prey and a pattern of search based upon the random walk ('the blundering idiot' model, Murdie, 1971).

LARVAL ANCHOVY BEHAVIOR AND FOOD DISTRIBUTION

A first-feeding larval anchovy is dependent for food on a very local scale. Its swimming and feeding behavior has been studied by Hunter (1972) in great detail. The pertinent results from his study relative to the capture of food is that feeding appears to be entirely visual and that, at first feeding, success of prey capture ranges from 10-30% of the micro-, phyto- and zooplankters attacked by the larva (Figure 1).

From laboratory and field work, Lasker (1975) showed that there is a critical threshold concentration of food particles for gut-filling by first-feeding anchovy larvae. At the prevalent oceanic temperature, 13-14°C in the anchovy's spawning ground, Lasker found that about thirty 40-50 μm particles/ml, were needed in the larva's immediate environment to stimulate feeding and gut filling. This is remarkably similar to prey concentrations which are determined from Vlymen's (1977) computer simulation for meeting the larva's energetic needs on the first day of feeding. In the laboratory, however, other factors for successful feeding are apparent and can modify these threshold concentrations. These were listed by Lasker (1975) as follows.

Particle Size at First Feeding Appears to be Critical

We know from the stomach content work on larval anchovies by Arthur (1976) as well as from investigations by Rojas de Mendiola (1974) on the larva of the Peruvian anchovy *E. ringens*, that these larvae can capture and eat particles as large as 100 μm in smallest dimension when they first begin to feed, but that the usual diet contains smaller particles with a minimum size ingested from 25 μm, and nauplii with an average width of 68 μm. Arthur (1976) mentions that about 20% of the food found in very early-stage anchovy larvae were "unidentified spheres ... probably of plant origin" but mostly, he and other workers describe copepod eggs and nauplii as dominant identifiable foods found in the larval intestine. For example, during the first few days of feeding, stomach contents revealed 43% of ingested particles were copepod nauplii; at 9 days of age, when the larva is 6 mm long, 68% of the food particles found are copepod

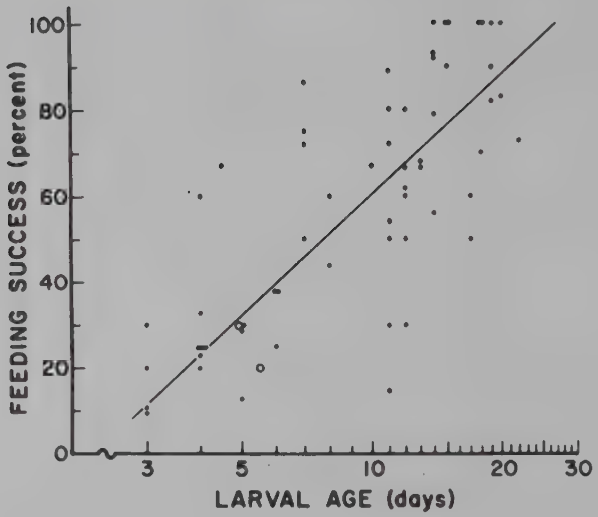

Figure 1. Feeding success (percent of attacked prey captured) of anchovy larvae of various ages fed *Brachionus*. Larval age is plotted on log scale, equation for line is percent success = 93.2 (log age) - 33.30. Two open circles, larvae fed *Gymnodinium* (from Hunter, 1972).

nauplii and at 14 days (ca. 8 mm long), 91% were nauplii*. Doubling the diameter of a spherical particle increases its volume 8 times. In the environment of the anchovy larva, this difference can have a profound effect on the feeding larva. For example, when feeding on small particles, the anchovy larva must capture (according to Hunter) approximately 230 forty-micron diameter particles a day. If the capture efficiency on the first day of feeding is 10%, the larva must attack 2,300 particles. However, the capture and digestion of a single 80 μm particle provides energy at least equivalent to 8 forty-micron particles. Large particles, however, are not captured with as high an efficiency as small ones and this lower efficiency is related to mouth size (Hunter, 1977). Hunter (1977) also shows that when the anchovy larva reaches 6 mm in size (approximately 9 days of age), its metabolism has reached a level whereby it cannot survive on small particles alone. Thus, in any analysis of the feeding environment, consideration of both particle size and particle concentration seems to be essential.

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*Gut content studies suffer from the uncertainty that particles found may be there because they could not be digested. However, the particle sizes actually ingested are pertinent in the following discussion.

The Number of Particles Per Unit Volume in the Anchovy Larva's Environment Must be Above a Minimum Concentration

Hunter (1977) evaluated two methods available for determining the food density requirements for survival of anchovy larvae using a simple searching model as well as laboratory density experiments. His conclusions were that laboratory density experiments yield higher food density requirements for survival of anchovy larvae than simple searching models, but that the former suffer from the possible existence of larval density dependent interactions and that the small experimental tank volume may limit the searching capacity of the larva. While the searching model is not affected by these variables, it is grossly affected by errors in the parameters and the assumptions required by the model.

Using laboratory-spawned, first-feeding anchovy larvae as a bioassay of sea water aboard ship, Lasker (1975) showed that gut filling by a first-feeding anchovy larva in natural water at 13-14°C only occurs when a density of about 30 forty-to-fifty micron particles/ml is present at first feeding. He verified this with laboratory experiments. As the larva grows and becomes a more efficient feeder, the number of particles per unit volume needed for feeding is less because the animal increases the size of the particles it takes and begins to ignore smaller ones. At least for first-feeding larvae, the results obtained by Lasker give a reasonable estimate of the minimum density of 40-50 μm particles required for first feeding by anchovy larvae. Vlymen (1977) has demonstrated, through a prey concentration random walk model and a Markov chain prey attack model, that there is a quantitative connection between the growth of a larva and geometric arrangement of prey in its environment. He concludes from his model that survival after the first day of feeding can be achieved at particle concentrations of between 14 and 32 forty-micron particles/cm^3 in a geometrically structured patchy environment with patches having a particle concentration of 32 particles/cm^3 and an interpatch region having concentrations 14 particles/cm^3. The radius of the patches, and the interpatch region used in Vlymen's simulation, are in centimeters, a scale which is not routinely sampled in the sea.

The Kind of Food Organism Determines Larval Survival and Growth

Scura and Jerde (1977) showed in a number of laboratory experiments that first-feeding Northern anchovy larvae will ignore and fail to feed on particles less than 20 μm in diameter. These included diatoms, whether single or in chains, and microflagellates, e.g., *Dunaliella* or *Tetraselmis*. Diatoms are rarely reported from gut content studies of anchovy larvae. In the event a particle is large enough to be seen and eaten by an anchovy larva, the nutritional and caloric content of the particle must be sufficiently high in the aggregate to provide for metabolism and growth. Lasker *et al.* (1970) also showed that there was a striking difference between the ability of various microzooplankton to support larval anchovy growth and survival. For example, veliger larvae of some snails supported no anchovy larva growth or survival, while the dinoflagellate *Gymnodinium splendens* and the rotifer *Brachionus plicatilis* could be used to rear the animal (Hunter, 1976). The dinoflagellate *Prorocentrum* does not support growth, as Scura and Jerde (1977) have shown, nor does the dinoflagellate *Gonyaulax polyedra*. *Prorocentrum* may simply be too small and not have enough calories per cell; but *Gonyaulax*, a larger cell, can be captured in great quantity by the larva and, although smaller than *Gymnodinium*, might have been expected to support growth and survival, but did not do so in laboratory experiments.

PROBABILITIES OF ENCOUNTER AT DIFFERENT DENSITIES

In this section, we suggest an approach which, when coupled with field information on the distribution of proper-sized food particles for first-feeding anchovy larvae, may provide a tool with which to determine the extent and goodness of fit of anchovy larvae feeding grounds. With this information, it may be possible to predict whether recruitment will be successful from any particular spawning.

Important features of anchovy larvae behavior have been pointed out above. The most important of these, for purposes of this discussion, are the threshold concentrations for feeding, the number of strikes a first-feeding larva makes in a day*, the percent success with which it can capture food, and the maximum size particle it can successfully ingest at first feeding. Although usually there is a hyperbolic distribution of particle size in ocean water with the largest particles being fewest in number (Vlymen, 1977), often in the environment of these larvae we find patches containing two or more specific size classes of particles together, e.g., copepod nauplii and dinoflagellates. As a first-feeding anchovy larva swims among these particles, it encounters the most prevalent organism most frequently and captures at least 10% of those at which it strikes. If the animal attacks a nauplius twice the diameter of a dinoflagellate in a hunting series and manages to capture it, the nauplius can provide as much as an order of magnitude more energy than the smaller particle on which it was feeding. Therefore, the feeding behavior of an individual anchovy larva is constrained by a) the concentration and kind of prey which will stimulate a feeding attack; b) the prey distribution; c) the physical and physiological limitation on the number of possible attacks; and d) the gut volume.

In the first analysis shown below, Vlymen's (1977) computer growth model** for Northern anchovy larvae is used with some modification to simulate a random distribution of two size ranges of particles, 45-55 μm and 95-105 μm in diameter. Therefore, on the first day of feeding, the larva is faced with a locally homogeneous environment containing a random selection of particles suitably sized for ingestion. The concentrations of the particles (Table 1) are such that they encompass the range for these sizes found by surveys in the Southern California Bight, the major spawning and feeding ground of the Northern anchovy. When one does this, concentrations of the two particles can be found that provide for metabolism at least, and growth when these concentrations are exceeded. This analysis assumes that the placement of large particles in the feeding queue of small particles is random, with the results given as the average growth rate for the population of first-feeding anchovy larvae on the first day.

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*Hunter and Thomas (1974) have shown that the rate of larval anchovy feeding increases with increasing food density. Strike rates of anchovy larvae can be as high as 10 per minute, but usually average 4 to 5 per minute. We use 10 strikes per minute in this simulation model.

**Some of the terminology employed (e.g., size specific capture rates) is more general than actually required for this paper. The mathematics and notation used were chosen in order to simplify the adaptation of Vlymen's work and in anticipation of further work on the same topic.

Table 1

Analysis of average growth in millimeters of anchovy larvae for the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 μm at 14.0°C, a 10% capture success rate and random distribution. Energy per each small particle is $4.236 * 10^{-5}$ cal. and for each large particles is $4.523 * 10^{-4}$ cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 μm particles/ml	Concentrations of 95-105 μm particles/ml					
	0.00	0.001	0.01	0.1	1.0	10.0
0.0	-0.08	-0.08	-0.08	-0.08	-0.08	-0.02
1.0	-0.08	-0.08	-0.08	-0.08	-0.08	-0.01
10.0	-0.08	-0.08	-0.08	-0.08	-0.07	-0.01
20.0	-0.07	-0.07	-0.07	-0.07	-0.07	-0.01
30.0	-0.07	-0.07	-0.07	-0.07	-0.06	0.00
40.0	-0.06	-0.06	-0.06	-0.06	-0.06	0.00
50.0	-0.06	-0.06	-0.06	-0.06	-0.05	0.01
60.0	-0.05	-0.05	-0.05	-0.05	-0.05	0.01
70.0	-0.05	-0.05	-0.05	-0.05	-0.04	0.01
80.0	-0.04	-0.04	-0.04	-0.04	-0.04	0.02
90.0	-0.04	-0.04	-0.04	-0.04	-0.03	0.02
100.0	-0.04	-0.04	-0.04	-0.03	-0.03	0.02
200.0	-0.03	-0.03	-0.03	-0.03	-0.02	0.01
300.0	-0.03	-0.03	-0.03	-0.03	-0.02	0.00

If the larva could attack all prey in its visual field, the expected number of captures, N_c, would be the product of the number N of potential attacks (excursions), the probability of attack PA, the probability $PS(S)$ of actually selecting organisms of size S (in this analysis $PS(S)=1$), the relative frequency $R(S)$ of organisms of size S in the prey distribution and the probability of capture $PC(S)$, i.e., where $E(N_c)$ is the average number of prey captured,

$$E(N_c) = N \; PA \sum_{s=\ell}^{u} PS(S) \; R(S) \; PC(S)$$

where $N \leq N_{max}$, and $\sum_{s=\ell}^{u}$ indicates a summation over all sizes of acceptable or available prey.

Vlymen's (1977) model corrects the attack and capture rates for delays between each. In other words, once an attack is made, there is a finite time before the next attack. This is taken into consideration in programming the survival and growth of anchovy larvae feeding on different sized particles; the attack probabilities are calculated as defined in the program diagrammed in Figure 2.

The expected volume V_c of captured organisms will be

$$E(V_c) = N\ PA \sum_{s=l}^{u} PS(S)\ R(S)\ PC(S)\ V(S)$$

where $N \leq N_{max}$

$V_c \leq V_{max}$.

When $V(S)$ is the volume of organisms of size S, the gross energy return GE_c will be

$$E(GE_c) = N\ PA \sum_{s=l}^{u} PS(S)\ R(S)\ PC(S)\ CAL(S)$$

where $CAL(S)$ is the calories per organism of size S and

$N \leq N_{max}$

$V_c \leq V_{max}$

S_1 = 45-55 μm; S_2 = 95-105 μm

N_{max} = 10 strikes/min = 600/hr. = 7200/12-hr. day

$PC(S)$ = constant for any length

$PS(S_1) = PS(S_2) = 1$

$N\ PA$ is calculated from Vlymen (1977) and is a function of total concentration

$TC = C_1 + C_2$ where C_1 = 1, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 200, and 300/ml and

C_2 = 0.001, 0.01, 0.1, 1.0 and 10.0/ml.

$$R(S_1) = \frac{C_1}{TC},\ R(S_2) = \frac{C_2}{TC}$$

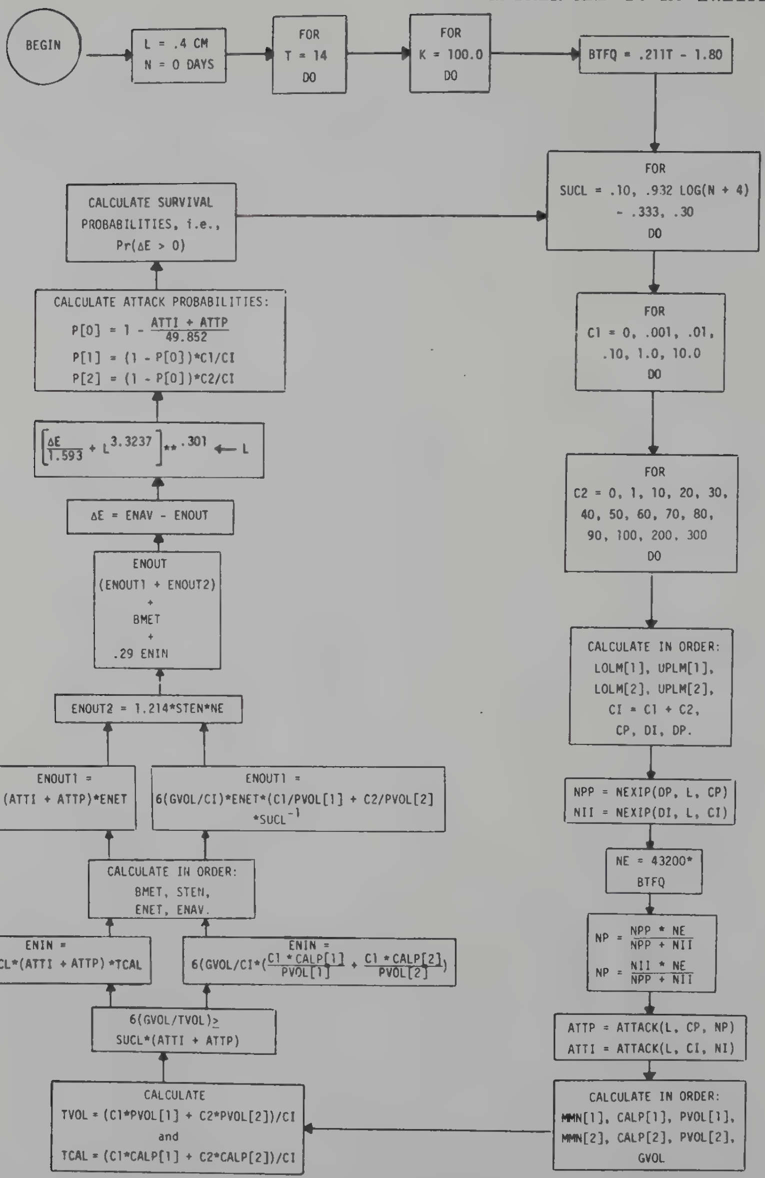
BEGIN
L = .4 CM
N = 0 DAYS
FOR T = 14 DO
FOR K = 100.0 DO
BTFQ = .211T - 1.80
FOR SUCL = .10, .932 LOG(N + 4) - .333, .30 DO
FOR C1 = 0, .001, .01, .10, 1.0, 10.0 DO
FOR C2 = 0, 1, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 200, 300 DO
CALCULATE IN ORDER: LOLM[1], UPLM[1], LOLM[2], UPLM[2], CI = C1 + C2, CP, DI, DP.
NPP = NEXIP(DP, L, CP)
NII = NEXIP(DI, L, CI)
NE = 43200* BTFQ
NP = (NPP * NE)/(NPP + NII)
NP = (NII * NE)/(NPP + NII)
ATTP = ATTACK(L, CP, NP)
ATTI = ATTACK(L, CI, NI)
CALCULATE IN ORDER: MMN[1], CALP[1], PVOL[1], MMN[2], CALP[2], PVOL[2], GVOL
CALCULATE TVOL = (C1*PVOL[1] + C2*PVOL[2])/CI and TCAL = (C1*CALP[1] + C2*CALP[2])/CI
6(GVOL/TVOL)≥ SUCL*(ATTI + ATTP)
ENIN = SUCL*(ATTI + ATTP)*TCAL
ENIN = 6(GVOL/CI*((C1*CALP[1])/PVOL[1] + (C1*CALP[2])/PVOL[2])
CALCULATE IN ORDER: BMET, STEN, ENET, ENAV.
ENOUT1 = (ATTI + ATTP)*ENET
ENOUT1 = 6(GVOL/CI)*ENET*(C1/PVOL[1] + C2/PVOL[2] *SUCL^-1
ENOUT2 = 1.214*STEN*NE
ENOUT (ENOUT1 + ENOUT2) + BMET + .29 ENIN
ΔE = ENAV - ENOUT
[ΔE/1.593 + L^3.3237]**.301 ← L
CALCULATE ATTACK PROBABILITIES:
P[0] = 1 - (ATTI + ATTP)/49.852
P[1] = (1 - P[0])*C1/CI
P[2] = (1 - P[0])*C2/CI
CALCULATE SURVIVAL PROBABILITIES, i.e., Pr(ΔE > 0)

Figure 2. Program modified after Vlymen (1977) for determining survival and growth of first-feeding larval anchovy in various food concentrations. Notation after Vlymen (1977) follows:

L = larval anchovy length, 4 mm
N = 0, first day of feeding
T = 14.0°C
K = dispersion coefficient of 100.00, i.e. random distribution of prey
BTFQ = temperature dependent excursion frequency
SUCL = age dependent success of capture function
C1 = concentration of small prey
C2 = concentration of large prey
LOLM = lower prey concentration limits
UPLM = upper prey concentration limits
CI = interpatch concentration
CP = intrapatch concentration
DP = patch diameter
DI = intrapatch distance
NEXIP (D,L,C) = number of steps required to traverse distance D in concentration of food particles C by larva of length L
NPP = NEXIP (DP,L,CP) = number of excursions a larva of length L will require to traverse a patch of radius DP and concentration CP
NII = NEXIP (DI,L,CI) = number of excursions a larva of length L will require to traverse an interpatch of radius DI and particle concentration CI
NE = number of excursions in 12 hours of foraging
NP = proportion of total daily foraging excursions spent in patches, and NI = in between patches
ATTACK (L,C,N) calculates the number of attacks on prey made by an anchovy larva of length L with N excursions in prey concentration C; NI, attacks between patches; NP, attacks in patches
CALP = caloric value of particles
MMN = size of particles
PVOL = volume of particle
GVOL = maximum gut volume of larva of length L
TVOL = total volume of particles eaten
TCAL = total calories of particles eaten
SUCL*(ATT1+ATTP) = particles successfully attacked
NE = number of excursions; excursions at night = 0.214 NE
STEN = energy per excursion
ENIN = energy in, or daily ration of calories
ENOUT1 = energetic debt of attacks
ENOUT2 = energetic debt of 24 hours of swimming, i.e. 1.214*NE*STEN
BMET = temperature and length dependent basal metabolic debt for 24 hours
ENAV = available energy or 0.48 ENIN
ENET = energy of attack = 3 STEN
0.29 ENIN = energy cost for mechanical processing of food
P[0] = probability of no attack
P[1] = probability of attack on small particle
P[2] = probability of attack on large particle

This simulation implies that the total number of particles in the larva's environment governs the frequency of strikes. The larger particles, even at their highest concentration, are ingested randomly (non-selectivity). Technically, despite the highest concentrations of the largest particles (e.g., nauplii), these must be taken very infrequently if the concentration of small particles is so high that the larger particles rarely show up in the feeding queue. Therefore, it is not the absolute concentration of the large particles that govern their capture by the larva, but rather their concentration relative to the larger number of small particles in the larval environment. Tables 1, 3 and 5 show the results of this simulation. A full discussion of these results is given in the following section.

A second analysis (Tables 2, 4 and 6) is based upon the same random arrangement of large particles among small particles, but

Table 2

Analysis of percent survival of anchovy larvae after the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 μm at 14.0°C and random distribution. Attack rate is 10 per minute and success of capture is 10%. Energy per each small particle is 4.236 * 10^{-5} cal. and for each large particle is 4.523 * 10^{-4} cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 μm particles/ml	Concentrations of 95-105 μm particles/ml					
	0.00	0.001	0.01	0.1	1.0	10.0
0.0	0.0	0.0	0.0	0.0	0.0	31.0
1.0	0.0	0.0	0.0	0.0	0.0	30.0
10.0	0.0	0.0	0.0	0.0	0.0	34.7
20.0	0.0	0.0	0.0	0.0	0.0	41.1
30.0	0.0	0.0	0.0	0.0	0.0	47.5
40.0	0.0	0.0	0.0	0.0	0.0	54.1
50.0	0.0	0.0	0.0	0.0	0.0	60.2
60.0	0.0	0.0	0.0	0.0	0.0	66.2
70.0	0.0	0.0	0.0	0.0	0.0	71.6
80.0	0.0	0.0	0.0	0.0	0.0	76.6
90.0	0.0	0.0	0.0	0.0	0.1	81.0
100.0	0.0	0.0	0.0	0.0	0.5	84.7
200.0	0.1	0.1	0.1	0.1	1.4	62.9
300.0	0.1	0.1	0.1	0.1	0.7	40.5

Table 3

Analysis of average growth in millimeters of anchovy larvae for the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 µm at 14.0°C, a 20% capture success rate and random distribution. Energy per each small particle is $4.236 * 10^{-5}$ cal. and for each large particle is $4.523 * 10^{-4}$ cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 µm particles/ml	Concentrations of 95-105 µm particles/ml					
	0.00	0.001	0.01	0.1	1.0	10.0
0.0	-0.08	-0.08	-0.08	-0.08	-0.07	0.07
1.0	-0.08	-0.08	-0.08	-0.08	-0.07	0.07
10.0	-0.07	-0.07	-0.07	-0.07	-0.05	0.08
20.0	-0.06	-0.06	-0.06	-0.05	-0.04	0.09
30.0	-0.04	-0.04	-0.04	-0.04	-0.03	0.10
40.0	-0.03	-0.03	-0.03	-0.03	-0.02	0.11
50.0	-0.02	-0.02	-0.02	-0.02	-0.00	0.12
60.0	-0.01	-0.01	-0.01	-0.01	0.01	0.13
70.0	0.00	0.00	0.00	0.01	0.02	0.14
80.0	0.02	0.02	0.02	0.02	0.03	0.15
90.0	0.03	0.03	0.03	0.03	0.04	0.15
100.0	0.04	0.04	0.04	0.04	0.05	0.16
200.0	0.06	0.06	0.06	0.06	0.07	0.13
300.0	0.06	0.06	0.06	0.06	0.06	0.10

the results are given in percent survival. Survival probabilities are calculated from the frequencies with which the 49,852 excursions (made by a larva in a 12-hour day) would end in an attack. Vlymen (1977) has assumed that "awareness" or conditions for an attack will occur when the number of particles within the visual field, K, is ≥ 1 and calculated this probability to be:

$$PA = Pr(K \geq 1) = 1 - e^{(-\lambda V_{pr})}$$

where V_{pr} is the volume of the visual field = $0.0159L^3$ where L, the length of the larva, is in centimeters and λ is concentration in number of prey per milliliter. The condition necessary for survival is that the energy balance $\Delta E \geq 0$; the available energy is calculated from the actual intake of N_1 small particles and N_2 large particles when food is limiting or from the maximum digestible volume of food estimated to be 6 * gut volume in a 12-hour day.

Table 4

Analysis of percent survival of anchovy larvae after the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 μm at 14.0°C and random distribution. Attack rate is 10 per minute and success of capture is 20%. Energy per each small particle is $4.236 * 10^{-5}$ cal. and for each large particle is $4.523 * 10^{-4}$ cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 μm particles/ml	Concentrations of 95-105 μm particles/ml					
	0.00	0.001	0.01	0.1	1.0	10.0
0.0	0.0	0.0	0.00	0.0	0.0	98.6
1.0	0.0	0.0	0.00	0.0	0.0	98.7
10.0	0.0	0.0	0.00	0.0	0.0	99.6
20.0	0.0	0.0	0.00	0.0	0.4	99.9
30.0	0.0	0.0	0.00	0.0	5.4	99.9
40.0	0.1	0.1	0.1	0.4	29.8	99.9
50.0	14.1	14.1	15.3	22.1	72.2	99.9
60.0	80.5	80.5	80.4	83.4	95.8	99.9
70.0	99.5	99.5	99.5	99.5	99.8	99.9
80.0	99.9	99.9	99.9	99.9	99.9	99.9
90.0	99.9	99.9	99.9	99.9	99.9	99.9
100.0	99.9	99.9	99.9	99.9	99.9	99.9
200.0	99.9	99.9	99.9	99.9	99.9	99.9
300.0	99.9	99.9	99.9	99.9	99.9	99.9

To simulate the conditions needed for survival (as opposed to average growth shown in Tables 1, 3 and 5), the following conditions must be met by the model: a) the energy balance is such that $\Delta E \geq 0$ (in Vlymen's notation $ENIN-ENOUT$), and b) the available energy is the smaller of either of two quantities, $ENIN = 0.48\,[N_1\,CAL(S_1) + N_2\,CAL(S_2)]$ (i.e., the actual catch) or when food is not limiting,

$$ENIN = \frac{6 * gut\ volume}{C_1 + C_2}\left[\frac{C_1\,CAL(S_1)}{V(S_1)} + \frac{C_2\,CAL(S_2)}{V(S_2)}\right].$$

For any realization k of a trinomial, the relative frequency $f(N_{0,k}, N_{1,k}, N_{2,k})$ of obtaining $N_{0,k}$, $N_{1,k}$ and $N_{2,k}$ attacks on particles is

Table 5

Analysis of average growth in millimeters of anchovy larvae for the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 μm at 14.0°C, a 30% capture success rate and random distribution. Energy per each small particle is $4.236 * 10^{-5}$ cal. and for each large particle is $4.523 * 10^{-4}$ cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 μm particles/ml	Concentrations of 95-105 μm particles/ml					
	0.00	0.001	0.010	0.1	1.0	10.0
0.0	-0.08	-0.08	-0.08	-0.08	-0.06	0.12
1.0	-0.08	-0.08	-0.08	-0.08	-0.06	0.12
10.0	-0.07	-0.07	-0.07	-0.06	-0.04	0.13
20.0	-0.06	-0.05	-0.05	-0.05	-0.03	0.14
30.0	-0.03	-0.03	-0.03	-0.03	-0.01	0.16
40.0	-0.01	-0.01	-0.01	-0.01	0.01	0.17
50.0	0.00	0.00	0.00	0.00	0.02	0.18
60.0	0.02	0.02	0.02	0.02	0.04	0.19
70.0	0.03	0.03	0.03	0.04	0.05	0.20
80.0	0.05	0.05	0.05	0.05	0.07	0.22
90.0	0.06	0.06	0.06	0.06	0.08	0.23
100.0	0.08	0.08	0.08	0.08	0.09	0.24
200.0	0.11	0.11	0.11	0.11	0.11	0.19
300.0	0.11	0.11	0.11	0.11	0.11	0.16

$$f(N_{0,k}, N_{1,k}, N_{2,k}) = \frac{N!}{N_{0,k}!\, N_{1,k}!\, N_{2,k}!} P_0^{N_{0,k}} P_1^{N_{1,k}} P_2^{N_{2,k}}$$

where N = total number of excursions made by the larva (obtained from tail beat frequencies),

$N_0 = N - N_1 - N_2$ is the number of excursions in which no attacks have been made,

P_1 = probability of attack on small particles,

P_2 = probability of attack on large particles, and

$P_0 = 1 - P_1 - P_2$ is the probability of no attacks.

Table 6

Analysis of percent survival of anchovy larvae after the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 µm at 14.0°C and random distribution. Attack rate is 10 per minute and success of capture is 30%. Energy per each small particle is $4.236 * 10^{-5}$ cal. and for each large particle is $4.523 * 10^{-4}$ cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 µm particles/ml	Concentrations of 95-105 µm particles/ml					
	0.00	0.001	0.01	0.1	1.0	10.0
0.0	0.0	0.0	0.0	0.0	0.0	99.9
1.0	0.0	0.0	0.0	0.0	0.0	99.9
10.0	0.0	0.0	0.0	0.0	0.3	99.9
20.0	0.0	0.0	0.0	0.0	7.2	99.9
30.0	0.0	0.0	0.1	0.6	43.1	99.9
40.0	31.0	31.0	31.9	42.3	87.7	99.9
50.0	97.1	97.1	97.1	97.4	99.5	99.9
60.0	99.9	99.9	99.9	99.9	99.9	99.9
70.0	99.9	99.9	99.9	99.9	99.9	99.9
80.0	99.9	99.9	99.9	99.9	99.9	99.9
90.0	99.9	99.9	99.9	99.9	99.9	99.9
100.0	99.9	99.9	99.9	99.9	99.9	99.9
200.0	99.9	99.9	99.9	99.9	99.9	99.9
300.0	99.9	99.9	99.9	99.9	99.9	99.9

The probabilities $P_0+P_1+P_2 = 1$ and the attacks plus no attacks equal total number of excursions, i.e., $N_0+N_1+N_2 = N$.

To estimate survival over the first day of life, all $f(N_{0,k}, N_{1,k}, N_{2,k})$ must be determined to satisfy

$$.48\ (N_{1,k}\ C_1+N_{2,k}C_2) > ENOUT \text{ when } N_{1,k}\ V_1+N_{2,k}\ V_2 \leq 6*gut\ volume$$

or

$$\frac{.48\ (N_{1,k}\ C_1+N_{2,k}C_2)\,6*gut\ volume}{N_{1,k}\ V_1+N_{2,k}\ V_2} > ENOUT$$

where $N_{1,k}\ V_1+N_{2,k}\ V_2 > 6*gut\ volume.$

In addition, since the maximum strike rate is 10/minute, we must impose the finite restriction that $N_1+N_2 \leq 12\ (hrs.) * 60\ (min/hr) * 10\ (strikes/min) = 7200$.

Although all of the $N(N-1)$ possible outcomes have a finite probability of occurrence, the number of calculations can be significantly reduced by considering only outcomes in the ranges:

$$N P_0 - m \sqrt{N P_0 (1-P_0)} < N_{0,k} < N P_0 + m \sqrt{N P_0 (1-P_0)}$$

$$N P_1 - m \sqrt{N P_1 (1-P_1)} < N_{1,k} < N P_1 + m \sqrt{N P_1 (1-P_1)}$$

$$N P_2 - m \sqrt{N P_2 (1-P_2)} < N_{2,k} < N P_2 + m \sqrt{N P_2 (1-P_2)}$$

where $N_{2,k} = N-N_{0,k} - N_{1,k}$ and where m represents the number of standard deviations and can be made as large as necessary. In this calculation, $m=4$ so that the probability of any outcome falling outside the range will be negligible except for the very lowest particle densities; i.e., for estimating survival of say <0.01%.

The probabilities P_0, P_1 and P_2 are determined as follows:

$P_0 = 1 - (ATTI + ATTP)/49{,}852$ (Figure 2)

where P_0 is the probability of no attacks and

$1 - P_0$ is the probability of attack on either large or small particles, and $ATTI + ATTP$ is the total number of attacks.

Then $P_1 = (1 - P_0) \left(\frac{C_1}{C_1 + C_2}\right)$

and $P_2 = (1 - P_0) \left(\frac{C_2}{C_1 + C_2}\right)$

where C_1 = concentration of small particles,

C_2 = concentration of large particles.

RESULTS OF SIMULATED FEEDING BY FIRST-FEEDING ANCHOVY LARVAE

Minimum survival by first-feeding anchovy larvae to a second day of feeding depends on threshold concentrations of small particles and not on the presence or absence of large particles. From Tables 2, 4 and 6, large particles can be seen to enhance survival, but even in the highest concentration of large particles ever recorded from the Northern anchovy larva's environment, about 0.3/ml, and with capture success set at the highest level possible (30%), anchovy larvae can neither grow nor survive the first day of feeding on a diet of large particles alone. A probable food environment that the larva encounters is a proportion of small to large food particles of 30:0.1 or 30:0.01 per milliliter. At 30 small particles per milliliter, no anchovy larvae will survive the first day (Table 6). Only when large particles become prevalent at this low concentration of small particles, i.e., when there are between 0.01 and 0.1/ml or 10 to 100 per liter, is there a small increase in survival, although average growth remains negative. However, the difference in growth and survival is striking when the larva has in its immediate environment 40 small particles per milliliter instead of 30. Survival in this instance is increased to 31% and large particles make little difference even in concentrations as high as 0.1 per milliliter. Above 0.1 per milliliter (100/L) of large food particles, survival becomes greatly enhanced as long as 40 small particles per milliliter are also present. At concentrations greater than 10/ml, the distance of a first-feeding larva from its nearest possible food item is within its perceptive field, 2.7 mm (Hunter, 1972). The distance at 30 and 40 particles per milliliter are 1.78 to 1.62 mm, respectively (Gallagher and Burdick, 1970). This may be a critical range for the larva.

It is clear from the simulation of a 10% capture success rate shown in Tables 1 and 2 that under virtually all concentrations and combinations of food, a concentration of nauplii not yet seen in the sea, 10/ml (10,000/L), is needed to insure reasonable survival to the second day of feeding. At 20 and 30% capture rates, there is good agreement with the experimental data of O'Connell and Raymond (1970) who found that there was good survival of young anchovy larvae at naupliar concentrations of 4000/L, also abnormally high when compared to concentrations found in the ocean.

P. E. Smith (personal communication) believes that survival after the first day of feeding, as deduced from field collections, can be as high as 75%. This value is encountered in this simulation in concentrations of prey frequently found in the sea in dinoflagellate blooms (i.e., where small particles are between 40 and 50/ml) and emphasizes the importance of spatial and temporal aggregations of food patches in the larva's environment.

When the capture success rate is low (10%, Tables 1 and 2), this increases the negative aspect of having large numbers of small particles available to the larva. It is evident that the larva is so occupied by attacks on energy-poor particles and that it rarely encounters and cannot capture enough large, energy-rich particles at this low capture success rate to survive or grow through the first day of feeding.

Tables 3 and 4 illustrate the results of an intermediate capture success rate, 20%. Positive growth is only achieved when 70-80 small food particles per milliliter are available (Table 3) and there is very little to be gained by having large particles in the environment unless they are in hundreds per liter. Survival (Table 4) is achieved at much lower concentrations of small particles with the critical value about 50/ml. Survival enhancement by large food particles occurs in this simulation when 10-100/L of these are present coincidentally with the larger number of smaller particles.

THE RELATION BETWEEN PHYTOPLANKTON AND ZOOPLANKTON SPATIAL DISTRIBUTION AND LARVAL ANCHOVIES IN THE SEA

It is logical to inquire to what extent the concentrations of small and large food particles needed for adequate survival and growth of first-feeding anchovy larvae are found in the Northern anchovy spawning ground during the spawning season, December through March.

Phytoplankton

In 1974, Lasker (1975) found that chlorophyll maximum layers occasionally contained particle densities which could provide good feeding for first-feeding anchovy larvae. For example, in a series of stations along the California coast near Los Angeles, the densities of the dinoflagellate *Gymnodinium splendens* induced feeding by first-feeding anchovy larvae (on shipboard) at concentrations from 34 to more than 300 per milliliter. *Gymnodinium* was present as an apparently continuous patch which extended along the coast approximately 100 kilometers. An important observation was that stormy conditions were found to disrupt these layers and reduce the minimum densities below threshold levels for larval anchovy first feeding.

In a later study, Lasker (1978) reported on an extensive survey made along the California and Baja California coasts in 1975 where he sought to detect areas of anchovy spawning where particle densities were above minimum thresholds for first-feeding larval anchovy. He found a remarkable patch of the dinoflagellate

Gonyaulax polyedra extending from at least Point Conception to the Mexican border, a distance of 300 kilometers. The seaward extent of this very large patch ranged from a few kilometers in December 1974 to 40 kilometers in January 1975; the latter extending across the Southern California Bight from the mainland shore to the Channel Islands.

The vertical distribution of dinoflagellate patches has been studied from time to time. Sharp chlorophyll maxima coincide with dinoflagellate maxima but, with current sampling gear, these patches seem to be many meters thick. However, Kiefer and Lasker (1975) analyzed the vertical migration of *Gymnodinium splendens* populations and got very sharp chlorophyll maxima only 1 to 2 meters thick (Figure 3). Visual sightings of dinoflagellate blooms at the surface often give the familiar red or rust color of a "red tide." In 1976, the rich Peruvian upwelling system experienced a vast bloom of *Gymnodinium splendens* which became so dense in some places that hydrogen sulfide was produced when the organisms died. In Peru this phenomenon is known as "aguaje" and extended from Pimental to Matarani, a distance of 2,000 kilometers, in a more or less continuous patch (B. Rojas de Mendiola and J. Valdivia of the Instituto del Mar del Peru, personal communication).

In 1975, when *Gonyaulax polyedra* was the dominant particle in the feeding size range of first-feeding anchovy larvae and *Gymnodinium splendens* similarly dominated the Peruvian upwelling system, it is tempting to speculate that *Engraulis mordax* first-feeding larvae ate *Gonyaulax* in numbers off California while the Peruvian anchovy first-feeding larvae, *Engraulis ringens*, were eating *Gymnodinium*. In the former, because of the poor nutritional value of *Gonyaulax*, a poor year class would have been expected while in the latter we would have expected to see a good year class. Complicating the *Gonyaulax* situation in 1975, however, was the fact that a massive upwelling in the midst of the anchovy spawning season destroyed the patches of *Gonyaulax* and in fact severely reduced particle concentrations below the threshold needed for gut filling and metabolic needs of first-feeding larvae. Indeed, the 1975 year class of the Northern anchovy was very poor compared to other years (Sunada, California Department of Fish and Game, personal communication) while the Peruvian anchovy showed a resurgence from previous low levels in its 1975 year class. While these are at present only single observations, they suggest that it may be worthwhile to investigate both particle densities and distribution and nutritional content of larval anchovy food to forecast whether a recruitment will be successful or not. Microzooplankton concentrations never exceeded 30 per liter in hundreds of samples taken during 1974 and 1975 in the California studies described above.

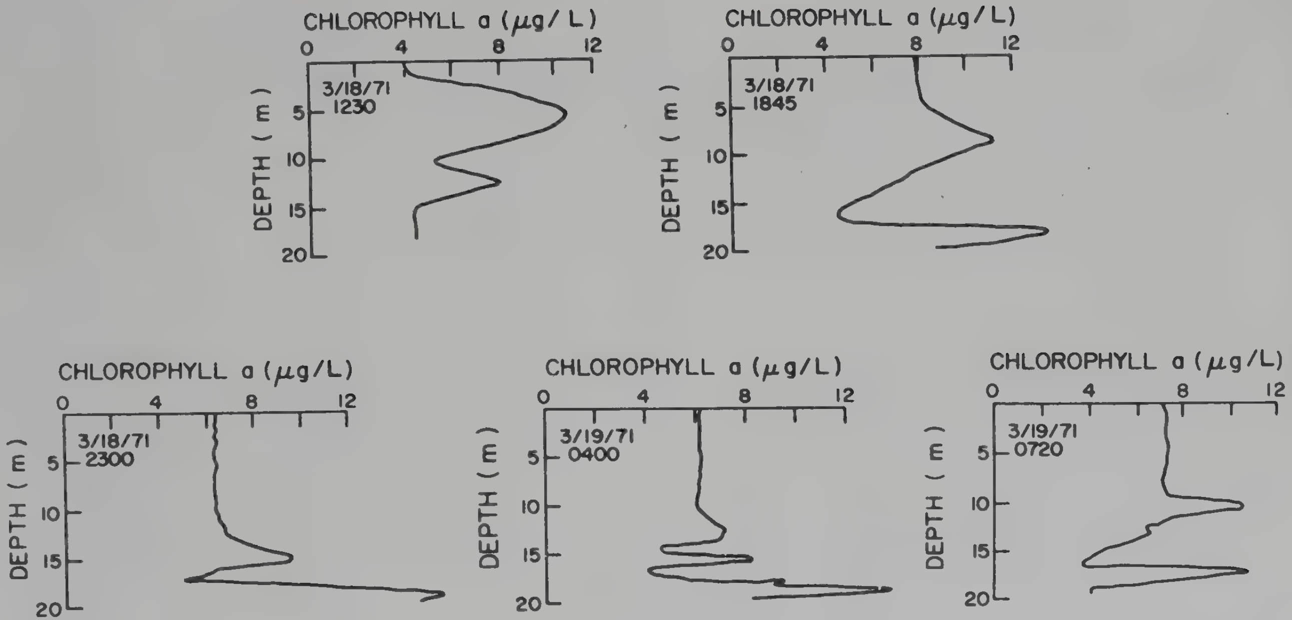

Figure 3. Profiles of the concentration of chlorophyll *a* based upon fluorescence profiles. The upper layer of *Gymnodinium splendens* at 1230 h was concentrated at 6 m; by 1845 it had moved to 8 m and reached 15 m by 2300. Movement upward commenced at 0200 reaching 10 m by 0720. The lower layer remained relatively close to the bottom during this time. Profiles were obtained in Coyote Bay, Bahia Concepcion, Mexico (lat. 26°43.0'N, long. 111°53.0'W) (from Kiefer and Lasker, 1975).

Zooplankton

When food is found in anchovy larvae intestines, it usually consists of copepod nauplii, copepod eggs and a variety of similarly small microzooplankters, regardless of where the anchovy population is found*. Yet, as we indicated before, the sampled densities of these potential food organisms have always seemed to be too low to maintain engraulids. This conflicting evidence leads one to believe that patches of microzooplankton may be prevalent in productive areas where anchovies are found, but present sampling gear underestimates the concentration factor. On occasion, when a sample of water is discovered to have a large number of nauplii or other microzooplankters, the sample, when retaken in the same place, does not duplicate the results. However, on one occasion, Lasker (1978) showed that in samples containing over 100 microzooplankters per liter taken 0.8 km apart, i.e., 2 and 2.8 km from the California shore, there was a remarkable coherence in the numbers and size distribution of copepod nauplii and post-naupliar copepods (Figure 4). This duplication indicated that a patch of at least 0.8 km in linear extent offshore was sampled despite a prevailing along-shore current. It should also be noted that motile phytoplankton food reproduce on an hourly or daily scale while nauplii are a stage in a copepod life cycle of several weeks. The predation on copepods by a major fish population like the Northern anchovy could cumulatively have a marked depressant effect on the local abundance of nauplii.

The point we wish to make is that temporal and spatial stability of the ocean is a prerequisite for successful feeding by clupeid larvae. Food organisms must have time to aggregate and, once patches are formed, they must have a sufficiently long life to permit larval fish feeding. However, it is much more likely that there will be aggregations of small particles than large ones and this in turn favors first day larval survival and growth.

The model described here to determine adequate feeding of various size particles for first-feeding anchovy larvae can be extended to older larvae as Vlymen (1977) has shown in his analysis of the effect of prey microdistribution to larval anchovy growth.

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*Most of the anchovy larvae examined have no food in their intestines. Whether this is due to rough treatment in plankton nets, to the severity of the usual Formalin preservation, or is the normal situation in the sea is not known. Kjelson *et al.* (1975) have shown, however, that menhaden larvae lose much of their gut contents with rough laboratory handling equivalent to field capture.

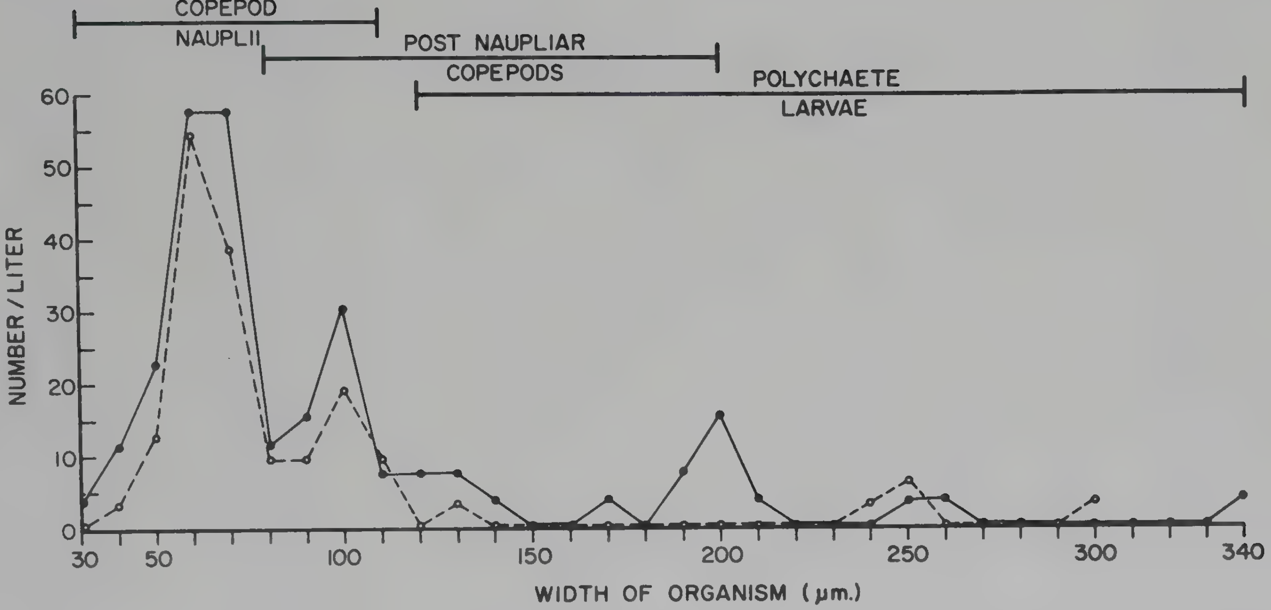

Figure 4. Width frequency distribution of two samples of microzooplankton taken from the chlorophyll maximum layer in March 1976, 0.8 km apart within 2 km of the shore off San Onofre, California. Closed circles indicate the sample taken nearest the shore which contained 280 microzooplankters per liter. The other sample contained 117 microzooplankters per liter. These were the only two of hundreds of pump samples taken in the Southern California Bight over a 3-year period which contained more than 100 microzooplankters per liter (from Lasker, 1978).

We know from the simulation presented in this paper that the enigma presented by the lack of reasonably large numbers of nauplii in the sea for larval anchovy food may be explained because the larvae don't need them, nor do the larvae encounter them with a sufficiently high frequency for these large particles to make more than a token contribution to survival and growth on the first day of feeding.

SUMMARY

Based on laboratory and field data, a simulation model of first-feeding anchovy larvae, *Engraulis mordax*, was constructed to investigate the effect of different prey size on survival and growth. First-feeding, naive anchovy larvae must depend almost entirely on small particles (ca. 45 μm diameter) for early survival, despite their ability to capture large particles. The absolute concentration of large particles (ca. 90 μm diameter) does not govern their capture by the larvae; rather, the more numerous small particles distract the larvae from capturing large particles. Simulation shows that a 10% prey capture efficiency will not suffice for survival or growth and that, at higher capture efficiencies (20-30%), there is a threshold of 30-50 small particles per milliliter needed for substantial survival and growth. Large particles, e.g., copepod nauplii, can enhance survival when they reach concentrations between 10 and 100 per liter in the same environment containing above-threshold numbers of small particles. An important distinction is made between survival and average growth; it is shown that larvae may survive in significant numbers in feeding regimes in which the average growth for the population is negative. These results are discussed in relation to actual field data from the spawning ground of the Northern anchovy.

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7823

Optimal Harvesting Strategies for Stochastic Single-Species, Multiage Class Models*

ROY MENDELSSOHN
Southwest Fisheries Center,
National Marine Fisheries Service, NOAA,
Honolulu, Hawaii 96812

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ABSTRACT

Qualitative properties of optimal harvesting policies for stochastic, single-species, multiage class models are described. For many problems the k-dimensional problem (k is the number of age classes) can be reduced to k one-dimensional problems, which can be solved far more readily. When such separability does not occur, bounds can be put on the derivatives of an optimal policy function which can greatly increase computational efficiency.

1. INTRODUCTION

In a series of recent papers, I have explored optimal policy functions for stochastic single-species, pooled-age-class models under a variety of assumptions on the one-period return. The basic results are given in [14]; these have been extended to include "smoothing costs" due to changes in the sizes of the harvest [12] and also to include multiple objectives [13]. The purpose of this paper is to extend this analysis to single-species, multiage class models.

The age distribution of the population affects harvesting strategies due to age-dependent mortality, reproduction, and size. For a given total population size x, the growth over the next years will vary greatly if the population is mainly in the younger rather than the older age classes. Mortality will vary. Reproduction due both to the first age of reproduction and to age-dependent reproductive rates will vary. The average weight of the catch will vary, since older animals tend to be larger also. Computer models that have been used to study the effects of management policies on sandhill

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cranes [15], elephants [7], and deer [1] show that age structure may have effects that are obscured by predictions based only on the total population size and the initial management policy.

A population model which includes the age distribution of the population raises conceptual problems with such traditional goals of resource management as maximum sustained yield. For example, a particular model of the population dynamics, for a given initial population distribution, may not permit any policy that ensures constant yield, constant total number harvested, or constant age distribution. Even if there exists a policy that realizes any or all of these goals, it may require a long span of time to bring the initial population into this equilibrium configuration, and the result may well be either under- or overexploitation of the resource during the nonequilibrium period. The problems encountered in trying to define a maximum sustained yield harvest for a Leslie matrix model of population growth is discussed by Mendelssohn [11]. This includes differing definitions given by Williamson [22], Watt [21], Usher [18], Dunkel [6], Doubleday [5], and Rorres and Fair [17]. The underlying dilemma in each of these articles is that of trying to extend to higher dimensions concepts that only have meaning in one dimension.

The models in this paper contain only limited biological detail as an initial examination of stochastic harvesting models with age structure. Deterministic models presented by Goh [8] and Clark et al. [3], to be described later in the paper, include age structure with very restrictive assumptions. Less restrictive models are presented in this paper, and they suggest possibilities and pitfalls for future research. For example, one might think that the results of Mendelssohn and Sobel [14] should extend into k-dimensions. Unfortunately, they do not. Some of the results of that paper rest on the fact that the real line is completely ordered by the inequality $\leqslant$. In other words, if x^1 is not less than or equal to x, then x^1 must be greater than x. However, coordinate-by-coordinate comparisons of k-vectors induce only partial orderings. For two k-vectors, $\mathbf{x}^1$ and $\mathbf{x}^2$, the falsity of $\mathbf{x}^1 \leqslant \mathbf{x}^2$ does not imply $\mathbf{x}^1 \geqslant \mathbf{x}^2$. Therefore, in higher dimensions, most of the proofs in [14] are invalid. As a result, the analyses in this paper are more complex, the assumptions are stronger, and the results weaker than those in that paper. Nevertheless, interesting results are obtained by using the same basic approach and methods as in that paper on two interesting classes of models. The first model assumes random recruitment and random age-dependent survivorship *rates*, both independent of population density. This model is a generalization of the classic Beverton-Holt model [2]. The second model differs from the first by assuming that recruitment is a random concave function of the total population size, analogous to the Ricker equation [16]. The first model has the mathematical property of "separability" or "additivity." As a result, it will be possible to find an optimal policy for each cohort independently of the rest of the population. A variety of weaker results are presented for the second model. The strongest result assumes that there is a linear return p^i from each age class, and that the sequence $\{p^i\}$, $i=1,\ldots,k$, is concave. With these assumptions, it is proven that an optimal policy has a "new better than used" (NBU) property, that is, the oldest are always harvested first.

Both models assume complete selectivity in harvesting the age classes. In practice, harvesting techniques lie between the two extremes of complete selectivity and random sampling. The assumption of complete selectivity allows a determination of the target if such control is possible, and lends insight into the crucial factors of the population dynamics if the best of all harvests is possible. One extension to include gear selectivity leads to "pulse" harvesting of the resource.

The notation here is the k-dimensional extension of that in [14]. Let the ith component x_t^i of the k-vector $\mathbf{x}_t=(x_t^i)$ denote the number alive in the ith age class at the beginning of period t. Similarly $\mathbf{y}_t$ ($\mathbf{z}_t$) is the vector of the number of individuals left (harvested) in the k age classes at the end of (during) period t. $\mathbf{d}_t$ is now a random vector whose components may be jointly distributed. The sequence $\mathbf{d}_1, \mathbf{d}_2, \ldots, \mathbf{d}_T$ is assumed to consist of independent and identically distributed random vectors distributed as the generic random vector $\mathbf{d}$. $A_t(\mathbf{x})$ denotes a k-vector-valued function, a policy function, with component functions $a_t^i(\mathbf{x})$, and $S[\mathbf{y},\mathbf{d}]$ is a k-vector valued (transition) function with components $s^i[\mathbf{y},\mathbf{d}]$. The one period return function $G(\mathbf{x},\mathbf{y})$ maps a subset of $\mathbb{R}^{2k}$ into $\mathbb{R}^1$. And finally, instead of (left) derivatives, the (left) gradient is evaluated. The gradient of a function f is written ∇f, and its ith component $\nabla^i f$. If f is a function mapping a subset of $\mathbb{R}^{2k}\to\mathbb{R}^1$, then $f^{[1]}$ is the gradient with respect to the first vector argument, and $f^{[2]}$ is the gradient with respect to the second vector argument. Thus, with obvious changes in interpretation, Eq. (4.1) in [14] remains the generic problem, that is:

$$
\begin{aligned}
&f_0(\cdot)\equiv 0,\\
&f_n(\mathbf{x})=\max_{0\leqslant \mathbf{y}\leqslant \mathbf{x}}\{J_n(\mathbf{x},\mathbf{y})\},
\end{aligned}
\tag{1}
$$

where

$$J_n(\mathbf{x},\mathbf{y})=G(\mathbf{x},\mathbf{y})+\alpha E\{f_{n-1}(S[\mathbf{y},\mathbf{d}])\}.$$

2. MODELS AND RESULTS

A model basic to fisheries research assumes constant recruitment each year, and survivorship functions which depend only on the size of each age class. Mathematically, this becomes

$$
\begin{aligned}
&x_{t+1}^1=R,\\
&x_{t+1}^{i+1}=s^i[y_t^i], \qquad i=1,\ldots,k-1.
\end{aligned}
$$

A special case of this model is the Beverton-Holt model [2], which has been discussed in the context of dynamic optimization by Goh [8] and Clark et al. [3].

Examples of fish populations that behave in a manner consistent with the Beverton-Holt model can be found in the references cited above or in [9] or [16]. However, it is rare that recruitment is truly constant, or that survivorship functions fit the data exactly; rather there is usually "noise" around this expected value. In the case of recruitment, this can be modeled by assuming that the constant (mean) level is modified by a random variable, that is,

$$x_{t+1}^1 = d^1 R, \qquad \infty > d^1 \geqslant 0$$

or

$$x_{t+1}^1 = R - d^1, \qquad 0 \leqslant d^1 \leqslant R.$$

In what follows, the multiplicative form d^1R will be assumed. There are two reasons for this. First, as has been discussed elsewhere [16, 20], if there are a large number of environmental effects acting on the number of recruits, then the random variable will tend to act multiplicatively and have a log normal distribution. Second, all the proofs presented for the multiplicative case are true for the additive case, with the obvious necessary modifications. Thus, it is without loss of generality that only the multiplicative case is examined here. The complete stochastic model can be described as

$$\begin{aligned} x_{t+1}^1 &= s^1[\mathbf{y},\mathbf{d}] = d^1R, \quad d^1R \geqslant 0 \qquad \text{for all } d^1, \\ x_{t+1}^{i+1} &= s^{i+1}[\mathbf{y},\mathbf{d}] = s^{i+1}[y^i, d^{i+1}], \qquad i = 1,\ldots,k-1. \end{aligned} \tag{2}$$

For the return from harvest, assume that the benefit is proportional to the weight of each class age, i.e., it is given by $\Sigma_{i=1}^k p^i(x^i - y^i)$, $p^i \geqslant 0$ for all i. If the cohorts are separated in space, as is often the case for ocean fish that spawn upriver, costs for harvesting each cohort should also be independent except for a per diem operating cost which is independent of whether harvesting is done. Let $g^i(x^i, y^i)$ be the cost of harvesting the ith age class from x^i to y^i individuals, and let $c\Sigma_{i=1}^k(x^i - y^i)$ be the total operating cost (that is, the cost is proportional to the time spent harvesting, which in turn is proportional to the total number harvested). Then the return function is

$$G(\mathbf{x},\mathbf{y}) = \sum_{i=1}^{k} \left\{ (p^i - c)(x^i - y^i) - g^i(x^i, y^i) \right\}. \tag{3}$$

The next theorem states that with the assumption of Eqs. (2) and (3), an optimal policy can be determined for each cohort independently. This is a useful result, because a k-dimensional problem has been reduced to k one-dimensional problems, where the stronger results of [14] apply.

THEOREM 1

In the dynamic program (1), *if* $S[\mathbf{y},\mathbf{d}]$ *is assumed to be given by Eq.* (2) *and* $G(\mathbf{x},\mathbf{y})$ *is assumed to be given by Eq.* (3), *then:*

(i) *the problem is divisible into k subprograms that consider each cohort independently;*
(ii) *for each* $n, t \geqslant n \geqslant k$, $a_n^i(\mathbf{x}) = a_n^i(x^i) = a^i(x^i)$ *for all* i *and* $\mathbf{x} \in X$, *where* $a_n^i(x^i)$ *denotes that* a_n^i *depends on* $\mathbf{x}$ *only through* x^i.

Proof. Part (i) is essentially proven in [19]. Part (ii) follows because for $n \geqslant k$, each cohort is independent of all other cohorts and $S[\mathbf{y},\mathbf{d}]$, $G(\mathbf{x},\mathbf{y})$ are stationary functions. ■

Theorem 1 does not describe an optimal policy but rather proves that the problem of finding an optimal policy can be greatly simplified. To see the usefulness of Theorem 1, consider the Beverton-Holt model as a special case of Eq. (2):

$$\begin{aligned} x_{t+1}^i &= d^1 R, \qquad d^1 R \geqslant 0, \\ x_{t+1}^{i+1} &= d^{i+1} s^i y_t^i, \quad 0 \leqslant d^{i+1} s^i \leqslant 1, \qquad i = 1, \ldots, k-1. \end{aligned} \tag{4}$$

The model assumes that given $d^{i+1}s^i$ a fixed proportion of the cohort survives to the next period, but that this proportion is "noisy", i.e., it varies at random from year to year. Note that the model does not meet the assumptions of two similar stochastic processes: first, where s^i is assumed to be a Bernoulli random variable, or second, where each individual, when born, has a known lifetime distribution. Assume that the return function is given by

$$G(\mathbf{x},\mathbf{y}) = \sum_{i=1}^{k} p^i (x^i - y^i), \qquad p^i \geqslant 0 \quad \text{for all } i. \tag{5}$$

THEOREM 2

For a dynamic programming problem given by Eq. (1), *if* $S[\mathbf{y},\mathbf{d}]$ *is given by Eq.* (4) *and* $G(\mathbf{x},\mathbf{y})$ *by Eq.* (5), *then:*

(i) *for each cohort born with n years remaining in the planning horizon, which can obtain a maximum age* $k(n)$ *within the planning horizon, there* *exists an age $j^*(n)$, $1 \leqslant j^*(n) \leqslant k(n)$, such that an optimal policy for the cohort is as follows:*

Age	*Action*
$1 \leqslant i \leqslant j^*(n)$	*Do not harvest.*
$j^*(n)$	*Harvest entire remaining cohort.*

(ii) *For $n \geqslant k$, $j^*(n) \equiv j$.*

Proof. From Theorem 1, the dynamic programming problem is separable by cohort. For each cohort, there is a dynamic program of $k(n)$ periods given by

$$f_0 \equiv 0,$$
$$f_i(x) = \max_{0 \leqslant y \leqslant x} \{p^{i} \cdot (x^i - y^i) + \alpha E f_{i+1}(d^{i+1} s y^i)\}, \qquad (6)$$
$$i = 1, \ldots, k(n).$$

The dynamic program (6) is separable by individual. The problem for each individual becomes

$$f_0 \equiv 0,$$
$$f_i(x) = \max\{p^i, \alpha E f_{i+1}(d^{i+1} s^i)\}, \qquad i = 1, \ldots, k(n), \qquad (7)$$

and the decision is either to harvest this period or not.

Given an individual just born Eq. (7) becomes

$$f_1 = \max\{p^1, E(d_n^2)\alpha p^2 s^1, E(d_n^2 d_{n-1}^3)\alpha^2 p^3 s^1 s^2, \ldots,$$
$$E(d_n^2 d_{n-1}^3 \ldots d_{n-k(n)-1}^{k(n)})\alpha^{k(n)-1} p^{k(n)} s^1 s^2 \ldots s^{k(n)-1}\}. \qquad (8)$$

Let $j^*(n)$ be the age where f_1 achieves its maximum; that is, $j^*(n)$ is the age where an individual of the cohort reaches a maximum value. From Eq. (8),

$$E(d_{n-1}^{i+1} \ldots d_{n-1-j^*(n)}^{j^*})\alpha^{j^*(n)-i-1} p^{j^*}(n) s^i \ldots s^{j^*(n)-1}$$
$$\geqslant E(d_{n-1}^{i+1} \ldots d^j)\alpha^{j-i-1} p^j s^i \ldots s^{j-1} \qquad (9)$$

for all i, $1 \leqslant i \leqslant j^*(n)$, and all j, $1 \leqslant j \leqslant k(n)$. From Eq. (7) for $i \leqslant j^*(n)$,

$$f_i = \max\{p^i, E(d_{n-1}^{i+1})\alpha p^{i+1} s^i, \ldots,$$
$$E(d_{n-1}^{i+1} d_{n-i-1}^{i+2} \ldots d_{n-k(n)-1}^{k(n)})\alpha^{k(n)-i-1} p^{k(n)} s^i s^{i+1} \ldots s^{k(n)-1}\}.$$

However, Eq. (9) implies that f_i achieves its maximum at age $j^*(n)$, and the proof of part (i) is complete.

Part (ii) follows immediately from Theorem 1, part (ii) and the result from part (i) of this theorem. ■

The policy described by Theorem 2 harvests a single age class each year. Since weight, length, and other measurements of size are usually well correlated with age, it is the type of target policy that might well be achieved in practice.

Goh [8] examines the Beverton-Holt model as a continuous-time, deterministic problem, and assumes that $s^i = s$ for all age classes and that $\{p^i\}$ is nondecreasing in i. Clark et al. [3] also assume that $s^i = s$ for all i, that $\{(p^{i+1} - p^i)/p^i\}$ is a nondecreasing sequence, and that harvesting removes each age class in proportion to its relative number in the population. Clark et al. use harvesting effort as their decision variable, and prove that "pulse"-type fishing is optimal, that is, in each period fishing effort should be either at a zero level or at a maximum level. The next corollary proves that if there is a function of effort which can be treated as a decision variable, and if the catch in each age class is proportional to this variable, then for $0 \leqslant e \leqslant e_{\max}$ (a constrained decision), an optimal policy chooses an effort of zero or $e_{\max}$.

COROLLARY

In the dynamic program (1) *let* $S[\mathbf{y},\mathbf{d}]$ *and* $G(\mathbf{x},\mathbf{y})$ *be given by Eqs.* (4) *and* (5), *respectively. Assume that in each period the only decision possible is total fishing effort* e *such that* $0 \leqslant e \leqslant e_{\max}$, *and that for a given* e *and an initial population vector* $\mathbf{x}$, *the catch from each age class in period* t *is* $eq_t^i x_t^i$. *Then an optimal policy in each period chooses either zero effort or else* $e_{\max}$.

Proof. The corollary will be proven by showing that the resulting dynamic programming problem is convex (linear) in the decision e. It then follows from [10] that the maximum must occur at a boundary point, that is, either $e_{\max}$ or zero. At period $n = 1$, the return is

$$e \sum_i p^i q_1^i x_1^i.$$

On the set $\{e : 0 \leqslant e \leqslant e_{\max}\}$ the return is linear and nondecreasing in e for all $\mathbf{x} \in X$, so that $e_{\max}$ is optimal in period 1, for all values of $\mathbf{x}$. At $n = 2$, for a given $\mathbf{x}$ and e, the return is:

$$e \sum_i p^i q_2^i x_2^i + \alpha E \left\{ e_{\max} \left[p^1 q_1^1 R + \sum_{i=1}^{k-1} p^{i+1} d^{i+1} s^i q_1^{i} \cdot \left(x_2^i - e q_2^i x_2^i \right) \right] \right\}$$

Again, the return is convex (linear) in e, so either $e_{\max}$ or zero is optimal. Assume the theorem is true in periods $2, 3, \ldots, n-1$. At period n, for given $\mathbf{x}$

and e, the return is

$$e\sum_i p^i q^i x^i + \alpha E f_{n-1}(S[\mathbf{x},e,\mathbf{d}]).$$

However, by the induction hypothesis and Eq. (4), $\alpha E f_{n-1}(S[\mathbf{x},e,\mathbf{d}]$ is convex in e, and the proof is complete. ■

In the fisheries literature the q_t^i's are called the catchability coefficients. The corollary relaxes the proof of Clark et al. [3] by allowing for age-dependent and time-dependent catchability. The crux of the proof is that the decision variable in each period is constrained neither by the state in that period nor by the decision in the period before.

Several authors (see the references in Sec. 1) have suggested that a Leslie matrix can model an exploited population that is at a level where resource limitations have no significant effect. Mendelssohn [10] demonstrates that an optimal policy for this model, assuming returns are linear, is either to harvest the entire population immediately or else to let the population grow without bound. The Beverton-Holt model assumes constant recruitment; the Leslie matrix assumes additive, proportional recruitment of the form $\sum F^i y^i$. A reasonable model might lie somewhere between these two models. As one possibility, consider recruitment given by a random, concave function, similar perhaps to the Ricker equation, and survivorship rates given by a random vector $\mathbf{ds}$ as in Eq. (3). Formally, the transition function becomes:

$$x_{t=1}^{1} = s^i\left[\sum_{i=1}^{k} y^i, d_t^1\right],$$

$$x_{t+1}^{i+1} = d_t^{i+1} s^i y_t^i, \quad 0 \leqslant d^{i+1} s^i \leqslant 1, \qquad i = 1,\ldots,k-1, \tag{10}$$

where $s^1[\cdot, d^1]$ is concave for each value of $\mathbf{d}$.

The next theorem examines harvesting strategies for the population model described in Eq. (10), with a linear return function as in Eq. (5). Part (a) of the theorem assumes $s^1[\cdot, d^1]$ is nondecreasing for each fixed $\mathbf{d}$. Consider an individual age i in some period. Then $\alpha^{j-i-1} p^j E(d^{i+1} d^{i+2} \ldots d^j) s^i s^{i+1} \ldots s^{j-1}$ is the expected discounted return from that individual at age j, without considering reproduction. If the expected discounted return at age j is greater than p^i, there is an optimal policy such that no individuals are harvested from that age class in that period.

Part (b) of the theorem assumes $d^{i+1} s^i = ds$ for all age classes i, but $s^1[\cdot, d^1]$ need not be nondecreasing. Then it is shown that for each period n and for all initial populations $\mathbf{x} \in X$, the total number remaining in the population satisfies

$$0 \leqslant \sum_{i=1}^{k} a^i(\mathbf{x}^1) - \sum_{i=1}^{k} a^i(\mathbf{x}) \leqslant \sum_{i=1}^{k} x^{1i} - \sum_{i=1}^{k} x^i \qquad \text{if} \quad \mathbf{x}^1 \geqslant \mathbf{x}.$$

Part (c) is similar to part (b), but it is assumed also that the p^i's form a concave sequence. This would be true if the growth curve were a concave function of time, as in the von Bertalanffy growth equation. With these assumptions, an optimal harvesting strategy has an NBU property, that is, an older individual is always harvested before a younger one.

THEOREM 3

In the dynamic program (1) *assume* $S[\mathbf{y},\mathbf{d}]$ *is given by Eq.* (10) *and* $G(\mathbf{x},\mathbf{y})$ *is given by Eq.* (5).

(a) *Suppose* $s^1[\cdot,\mathbf{d}]$ *is nondecreasing, continuous, and concave for each* **d**, *and let* $k^i(n)$ *be the largest age obtainable by an individual of age i in period n. Suppose that for some j width*

$$i<j\leq k^i(n),$$

$$\alpha^{j-i-1}E\left(d_n^{i+1}d_{n-1}^{i+2}\ldots d_{n-j-1}^{j}\right)p^js^is^{i+1}\ldots s^{j-1}\geq p^i. \tag{11}$$

Then no individuals are harvested from age class i in period n.

(b) *If* $s^1[\cdot,\mathbf{d}^1]$ *is concave and continuous, and if* $d^{i+1}s^i=ds$ *for all i,* $i=1,\ldots,k-1$, *then for each n and all* $\mathbf{x}\in X$,

$$0\leq\sum_{i=1}^{k}\alpha^i(x^1)-\sum_{i=1}^{k}\alpha^i(x)\leq\sum_{i=1}^{i}x^{1i}-\sum_{i=1}^{k}x^i \qquad \text{if} \quad x^1\geq x.$$

(c) *If, under the assumption of part* (b), *it is assumed that the sequence* $\{p^i\}$ *is concave in i, then an NBU policy is optimal.*

Proof. Essential to the proof of this theorem is that the theorem in [14] readily extends to k dimensions. This implies that $J_n(\mathbf{x},\mathbf{y})$ is concave and continuous, and that $f_n(\mathbf{x})$ is concave, continuous, and nondecreasing. Also, consider

$$\text{Maximize} \quad E\sum_{t=1}^{T}\sum_{i=1}^{k}\alpha p^i(x_t^i-y_t^i) \tag{12}$$

subject to $0\leq\mathbf{y}_t\leq\mathbf{x}_t$ and Eq. (10). Substituting $S[\mathbf{y}_{t-1},\mathbf{d}]$ for $\mathbf{x}_t$, $t=2,\ldots,T$, Eq. (12) becomes

$$\text{Maximize} \quad E\left\{\sum_{t=1}^{T}\sum_{i=1}^{k}\alpha^{t-1}p^i(s^{i-1}[\mathbf{y}_t,\mathbf{d}_t]-y_t^i)+\sum_{i=1}^{k}p^ix_1^i-\alpha^{T-1}\sum_{i=1}^{k}p^iy_T^i\right\}. \tag{13}$$

The term $\sum_{i=1}^{k} x_1^i$ is independent of the decision process, and Eq. (13) clearly obtains a maximum at $\mathbf{y}_T \equiv 0$. Let $G(\mathbf{y})$ be given by

$$G(\mathbf{y}) = \sum_{i=1}^{k} p^i(\alpha E(s^{i-1}[\mathbf{y},\mathbf{d}] - y^i)).$$

Then the dynamic programming problem becomes

$$\begin{aligned} &f_0(\cdot) \equiv 0, \\ &f_n(x) = \max_{0 < \mathbf{y} < \mathbf{x}} \{G(\mathbf{y}) + \alpha E f_{n-1}(S[\mathbf{y},\mathbf{d}])\}. \end{aligned}$$

Let $J_n(\mathbf{y})$ be defined as

$$G(\mathbf{y}) + \alpha E f_{n-1}(S[\mathbf{y},\mathbf{d}]).$$

Part (a). At period $n=1$,

$$\nabla^i J_1(\mathbf{y}) = \alpha E(d^{i+1}) p^{i+1} s^i - p^i + \alpha p^1 E s^{[1]}\Big[\sum y^i, d^1\Big].$$

Assume, as in the theorem, that $\alpha E(d^{i+1}) p^{i+1} s^i - p^i$ is nonnegative. By assumption, $s^{[1]1}\,[\sum y^i, d^1]$ is nonnegative, so that $\nabla^i J_1(\mathbf{y})$ is nonnegative for all $\mathbf{y}$. From the necessary and sufficient conditions for an optimum [10], this implies that $a_1^i(\cdot) \equiv x^i$.

Assume the theorem is true in periods 1, 2, 3, ..., n − 1. At period n,

$$\nabla^i J_n(\mathbf{y}) = \alpha E(d^{i+1}) p^{i+1} s^i - p^i + \text{terms nonnegative for all } \mathbf{y}. \tag{14}$$

If $\alpha E(d^{i+1}) p^{i+1} s^i - p^i$ is nonnegative, the theorem is immediate. If not, and there exists an age j such that Eq. (11) is true, then it follows that

$$\alpha^{j-i-1} E(d^{i+1} d^{i+2} \ldots d^j) p^j s^i s^{i+1} \ldots s^{j-1} \geqslant p^i > \alpha E(d^{i+1}) p^{i+1} s^i. \tag{15}$$

From the inductive hypothesis, this equation implies that no individuals are harvested from age class $i+1$ in period $n-1$. Therefore, Eq. (14) becomes

$$\begin{aligned} \nabla^i J_n(\mathbf{y}) = {} & \alpha^2 E(d^{i+1} d^{i+2}) p^{i+2} s^i s^{i+1} - p^i \\ & + \text{terms nonnegative for all } \mathbf{y}. \end{aligned}$$

Again, either $\alpha^2 E(d^{i+1} d^{i+2}) p^{i+2} s^i s^{i+1} - p^i$ is nonnegative, or else the same argument can be repeated up to age j, where the expression is nonnegative by assumption. Thus $\nabla^i J_n$ is nonnegative for all y, and this implies that $a_n^i(\cdot) \equiv x^i$ for all $\mathbf{x} \in X$.

Part (b). Consider the transformation of variables

$$\begin{aligned} w_t^1 &= x_t^1, & v_t^1 &= y_t^1, \\ w_t^2 &= x_t^1 + x_t^2, & v_t^2 &= y_t^2 + y_t^1, \\ &\vdots & &\vdots \\ w_t^k &= \sum_{i=1}^{k} x_t^i, & v_t^k &= \sum_{i=1}^{k} y_t^i. \end{aligned}$$

Then the dynamic programming problem becomes

$$\begin{aligned} & f_0(\cdot) \equiv 0, \\ & f_n(\mathbf{w}) = \max_{\substack{w^{i+1} - w^i \geqslant v^{i+1} - v^i \geqslant 0 \\ i = 1, \ldots, k-1}} \{J_n(\mathbf{v})\} \end{aligned}$$

where

$$J_n(\mathbf{v}) = \sum_{i=1}^{k} c^i v^i + \alpha E f_{n-1}(S[\mathbf{v}, \mathbf{d}])$$

and

$$c^i = (\alpha \mu s p^{i+2} - p^{i+1}) - (\alpha \mu s p^{i+1} - p^i), \qquad \mu \equiv E(d)$$

$S[\mathbf{v}, \mathbf{d}]$ is given by

$$\begin{aligned} & s^1[\mathbf{v}, \mathbf{d}] = s^1[v^k, d^1] \\ & s^j[\mathbf{v}, \mathbf{d}] = s^1[v^k, d^1] + ds \sum_{i=1} (v^{i+1} - v^i), \qquad j = 2, \ldots, k-1. \end{aligned}$$

Suppose $v^k, v^{k-1}, \ldots, v^2$ are fixed. Then there is an optimal v^1 given by $v^{1*}(\mathbf{w}, v^k, v^{k-1}, \ldots, x^2)$. Now suppose $v^k, \ldots, v^3$ are fixed. Then there is an optimal v^2 depending only on $\mathbf{w}$ and $v^k, v^{k-1}, \ldots, v^3$. This can be repeated until the problem is reduced to choosing an optimal v^k given $\mathbf{w}$, and then unraveling the optimal $v^{k-1}, v^{k-2}, \ldots, v^1$. Noting that $\mathbf{w}$ affects the return only through the constraint set, it is tedious but straightforward to prove for $\mathbf{w}^1 \geqslant \mathbf{w}$, with $(w^{1i+1} - w^{1i}) \geqslant (w^{i+1} - w^i)$ for all i, that $v_n^k(\mathbf{w}^1) \geqslant v_n^k(\mathbf{w})$. This implies

$$\sum_{i=1}^{k} a_n^i(\mathbf{x}) \leqslant \sum_{i=1}^{k} a_n^i(\mathbf{x}^1) \qquad \text{if} \quad \mathbf{x}^1 \geqslant \mathbf{x}. \tag{16a}$$

A similar transformation of variables (summing over the age classes) can be done when $\mathbf{z} = \mathbf{x} - \mathbf{y}$ is the decision variable, and a parallel argument yields

$$\sum_{i=1}^{k}\left[x^{i}-a_{n}^{i}(\mathbf{x})\right]<\sum_{i=1}^{k}\left[x^{1i}-a_{n}^{i}(\mathbf{x}^{1})\right] \qquad \text{if} \quad \mathbf{x}^{1}\geqslant\mathbf{x}. \tag{16b}$$

Together, the two inequalities (16a) and (16b) yield:

$$0<\sum_{i=1}^{k} a_{n}^{i}(\mathbf{x}^{1})-\sum_{i=1}^{k} a_{n}^{i}(\mathbf{x})<\sum_{i=1}^{k} x^{1i}-\sum_{i=1}^{k} x^{i} \qquad \text{if} \quad \mathbf{x}^{1}\geqslant\mathbf{x}.$$

Part (c). By assumption $\{p^{i}\}$ is concave in i, which implies that the sequence $\{p^{i+1}-p^{i}\}$ is a nonincreasing sequence. For some constant s, $1\geqslant s\geqslant 0$,

$$\begin{aligned}(p^{i+1}-p^{i})\geqslant(p^{i+2}-p^{i+1}) \quad &\Rightarrow \quad (p^{i+1}-p^{i})\geqslant s(p^{i+2}-p^{i+1})\\ &\Rightarrow \quad (sp^{i+1}-p^{i})\geqslant(sp^{i+2}-p^{i+1}).\end{aligned} \tag{17}$$

Part (c) will be proven by showing that for each n and all $\mathbf{y}$, $\nabla^{i}J_{n}(\mathbf{y})\geqslant\nabla^{j}J_{n}(\mathbf{y})$ if $i<j$. If the inequality is true for all $\mathbf{y}$, then it follows that an individual will be harvested from age class j before any are harvested from age class i, which is the desired NBU policy.

At period 1,

$$\nabla^{i}J_{1}(\mathbf{y})=\alpha E(d)p^{i+1}s-p^{i}+\alpha p^{i}Es^{[1]1}\left[\sum y^{i},d^{1}\right]$$

and

$$\nabla^{i}J_{1}(\mathbf{y})-\nabla^{j}J_{1}(\mathbf{y})=\alpha E(d)s(p^{i+1}-p^{j+1})-(p^{i}-p^{j}). \tag{18}$$

Equation (18) is of the form $(sp^{i+1}-p^{i})-(sp^{j+1}-p^{j})$, $1\geqslant s\geqslant 0$. For $i<j$, Eq. (17) implies that this must be nonnegative, so that (18) is nonnegative for all $i<j$.

Assume the theorem is true at periods $1,2,3,\ldots,n-1$. At period n,

$$\begin{aligned}\nabla^{i}J_{n}(\mathbf{y})-\nabla^{j}J_{n}(\mathbf{y})=&\left\{\left[\alpha E(d)sp^{i+1}-p^{i}\right]-\left[\alpha E(d)sp^{j+1}-p^{j}\right]\right\}\\ &+\alpha sE\left\{d\left[\nabla^{i+1}f_{n-1}(S[\mathbf{y},\mathbf{d}])-\nabla^{j+1}f_{n-1}(S[\mathbf{y},\mathbf{d}])\right]\right\}.\end{aligned}$$

Equation (17) implies that the first term on the RHS of Eq. (19) is nonnegative. An argument similar to that in [14] implies

$$\nabla^{i+1}f_{n-1}(\mathbf{x})=\left[\nabla^{i+1}J_{n-1}(A_{n-1}(\mathbf{x})\right]^{+}. \tag{20}$$

By the inductive hypothesis, $\nabla^{i+1}J_{n-1}\geqslant\nabla^{j+1}J_{n-1}$ for all $\mathbf{y}$ if $i\leqslant j$. This implies that $\nabla^{i+1}f_{n-1}(\mathbf{x})\geqslant\nabla^{j+1}f_{n-1}(\mathbf{x})$ for all $\mathbf{x}\in X$ and that Eq. (19) is nonnegative if $i<j$. As noted at the start of the proof, the ordering of the gradient by age is sufficient to prove that an NBU policy is optimal. ■

The next theorem proves that if $s^1[\cdot, d^1]$ is nondecreasing, then the assumptions of Theorem 3, part (c) imply $A_{n+1}(\mathbf{x}) \geqslant A_n(\mathbf{x})$.

THEOREM 4

The assumptions of Theorem 3, part (c) *and the additional assumption that* $s^1[\cdot, d^1]$ *is nondecreasing imply that there is an optimal policy such that for each n and all* $\mathbf{x} \in X$,

(i) $A_{n+1}(\mathbf{x}) \geqslant A_n(\mathbf{x})$
(ii) *as* $n \to \infty$, $A_n(\mathbf{x}) \to A(\mathbf{x})$

Proof. $\nabla[f_1(\mathbf{x}) - f_0(\mathbf{x})] = \nabla f_1(\mathbf{x}) \geqslant \mathbf{0}$. Assume as an inductive hypothesis that $\nabla[f_n(\mathbf{x}) - f_{n-1}(\mathbf{x})] \geqslant \mathbf{0}$. Then

$$\nabla J_{n+1}(\mathbf{y}) - \nabla J_n(\mathbf{y}) = \alpha E\{[\nabla f_n(S[\mathbf{y}, \mathbf{d}]) - \nabla f_{n-1}(S[\mathbf{y}, \mathbf{d}])]\xi_d(\mathbf{y})\} \geqslant \mathbf{0}. \tag{21}$$

where $\xi_d(\mathbf{y})$ is the Jacobian matrix of $S[\mathbf{y}, \mathbf{d}]$ for fixed $\mathbf{d}$. Equation (21) implies that $\nabla J_{n+1}(A_n(\mathbf{x})) \geqslant \nabla J_n(A_n(\mathbf{x}))$. Since an NBU policy is an optimal policy, if $A_n(\mathbf{x})$ is to be altered in order to obtain an optimum in period $n+1$, it must be altered by increasing the oldest nonzero age class. This implies that $A_{n+1}(\mathbf{x}) \geqslant A_n(\mathbf{x})$.

To complete the induction, it is necessary to prove that $\nabla f_{n+1}(\mathbf{x}) - \nabla f_n(\mathbf{x}) \geqslant \mathbf{0}$. From the definition of $f_n(\mathbf{x})$,

$$\nabla^i f_{n+1}(\mathbf{x}) - \nabla^i f_n(\mathbf{x}) = \{[\nabla^i J_{n+1} A_{n+1}(\mathbf{x})]^+ - [\nabla^i J_n A_n(\mathbf{x})]^+\}.$$

If $a_n^i(\mathbf{x}) \neq x^i$, then $\nabla^i f_n(\mathbf{x}) = 0$, and it is trivially true that $\nabla^i f_{n+1}(\mathbf{x}) \geqslant \nabla^i f_n(\mathbf{x})$. If $a_n^i(\mathbf{x}) = x^i$, then $a_n^i(\mathbf{x}) = a_{n+1}^i(\mathbf{x}) = x^i$. It is possible that in this instance, $\nabla^i f_{n+1}(\mathbf{x}) \leqslant \nabla^i f_n(\mathbf{x})$. However, for the induction, what is important is that $a_{n+1}^i(\mathbf{x}) = x^i$ if $a_n^i(\mathbf{x}) = x^i$, that is, that $\nabla^i f_{n+1}(\mathbf{x})$ be positive. *This* is implied by the induction, and therefore it is without loss of generality that $\nabla^i f_{n+1}(\mathbf{x}) \geqslant \nabla^i f_n(\mathbf{x})$. This completes the proof of (i). The proof of (ii) is an immediate consequence of (i). Since $\{A_n(\mathbf{x})\}$ is a monotone nondecreasing sequence in n which has $\mathbf{x}$ as uniform upper bound, as $n \to \infty$ there exists an $A(\mathbf{x})$ such that $A_n(\mathbf{x}) \to A(\mathbf{x})$. ■

As in [14], the results of Theorems 3 and 4 can be used to increase computational efficiency as well as to lend insight into optimal harvesting strategies. The assumptions given in Theorem 3, part (c) yield the most complete results, so that model will be used to illustrate how the results improve computational efficiency.

There are two sets of results that apply. First, for each n and for all $\mathbf{x} \in X$,

$$0 \leqslant \sum_{i=1}^{k} a_n^i(\mathbf{x}^1) - \sum_{i=1}^{k} a_n^i(\mathbf{x}) \leqslant \sum_{i=1}^{k} x^{1i} - \sum_{i=1}^{k} x^i \qquad \text{if} \quad \mathbf{x}^1 \geqslant \mathbf{x}.$$

Also, for each n, $A_n(\cdot)$ has an NBU structure. For each n, $A_n(\mathbf{0}) \equiv \mathbf{0}$ starts the algorithm. Given $A_n(\mathbf{x})$, consider $A_n(\mathbf{x}+\boldsymbol{\delta}^j)$, where $\boldsymbol{\delta}^j$ is a k-vector with zero in every component but the jth, which has a value of one. Let j^* be the last nonzero age class of $A_n(\mathbf{x})$. Then if $j \geqslant j^*$, $A_n(\mathbf{x}+\boldsymbol{\delta}^j) \equiv A_n(\mathbf{x})$. If $j < j^*$, then $a_n^i(\mathbf{x}+\boldsymbol{\delta}^j) = a_n^i(\mathbf{x})$ for $i \neq j, j^*$; $a_n^j(\mathbf{x}+\boldsymbol{\delta}^j) = a_n^j(\mathbf{x})+1$, and $a_n^{j^*}(\mathbf{x}+\boldsymbol{\delta}^j)$ is either $a_n^{j^*}(\mathbf{x})$ or $a_n^{j^*}(\mathbf{x})-1$. Thus, given $A_n(\mathbf{x})$, either $A_n(\mathbf{x}+\boldsymbol{\delta}^j)$ is completely determined, or else only two states, $A_n(\mathbf{x})+\boldsymbol{\delta}^j$ and $A_n(\mathbf{x})+\boldsymbol{\delta}^j-\boldsymbol{\delta}^{j^*}$, need to be evaluated.

In the infinite horizon problem, the convergence of $A_n(\mathbf{x})$ to $A(\mathbf{x})$ may allow $A(\mathbf{x})$ to be calculated by linear programming (see [4] for details). However, it should be noted that the convergence of $A_n(\mathbf{x})$ to $A(\mathbf{x})$ does not necessarily imply that $f_n(\mathbf{x})$ converges to an $f(\mathbf{x})$ for which $A(\mathbf{x})$ is an optimal stationary policy.

3. DISCUSSION AND COMMENTS

The results presented here generalize to specific multiage class models the results of [14]. The interpretations of the results presented here are close enough to the discussion in that paper that it will not be repeated here.

There are several results that would seem to be true, but so far have escaped proof. They are of interest both as areas of future research and also as a means of examining more closely the models discussed in this paper.

Consider the most general form of the model described in Theorem 3, that is,

$$x_{t+1}^1 = s^1\left[\sum y_t^i, d^1\right],$$
$$x_{t+1}^{i+1} = d^{i+1} s^i y_t^i.$$

It would seem reasonable that for $n \geqslant k$, the elements of the gradients of $J_n(\mathbf{y})$ should remain in a constant ordering. For $n < k$, the ordering changes because the oldest obtainable age class varies, and therefore the future value of the age class varies. For $n > k$, consider $\nabla^i J_n(\mathbf{y})$:

$$\nabla^i J_n(\mathbf{y}) = \alpha E(d^{i+1}) s^i p^{i+1} - p^i$$
$$+ \alpha E\left\{\nabla^1 f_{n-1}(S[\mathbf{y},\mathbf{d}]) s^{[1]i}\left[\sum y^i, d^1\right]\right\}$$
$$+ \alpha s^i E\left\{d^{i+1} \nabla^{i+1} f_{n-1}(S[\mathbf{y},\mathbf{d}])\right\}.$$

Only the last term will vary as $\mathbf{y}$ or n changes for any two age classes. The last term is the expected future change in value due to future reproduction and future growth. That the ordering of the change in future growth should remain invariant after k years has an intuitive appeal in terms of the population dynamics.

For the same problem, it would seem to be true that

$$0 \leqslant \frac{\partial a_n^i(\mathbf{x})}{\partial x^i} \leqslant 1, \tag{22}$$

$$-1 \leqslant \frac{\partial a_n^i(\mathbf{x})}{\partial x^j} < 0 \qquad \text{for all} \quad (i,j),\ i \neq j.$$

Equation (22) has been proven for the special case of $d^{i+1}s^i = ds$ for all $i = 1, \ldots, k-1$. For the more general model, it is possible to prove that $0 \leqslant \partial a_n^i(\mathbf{x})/\partial x^i \leqslant 1$, and also that $0 \geqslant \partial a_n^i(\mathbf{x})/\partial x^j$ for $i \neq j$. However, the lower bound has not been proven. The motivation for the lower bound is that individuals in each age class are substitutes for one another. The future discounted growth in weight of an individual is density-independent. Reproduction only depends on the total number in the population. An optimal policy should substitute a less valuable individual (in the future) in the harvest for a more valuable one, if the additional individual is available. The reason why the substitution should be at most 1:1 is that reproductive return is being balanced by the substitution, and this only depends on the total number remaining. While this argument may seem intuitively correct, no proof or counterexample has been found yet.

If $s^1[\cdot, d^1]$ is nondecreasing, it would seem that for all $n \geqslant k$, $A_{n+1}(\mathbf{x}) \leqslant A_n(\mathbf{x})$ for all $\mathbf{x} \in X$. Again, the argument hinges on the idea that after k periods the "end effects" due to a finite planning horizon disappear. The proof would be similar in spirit to Theorem 3, but it would have to be able to evaluate $\nabla f_k(\mathbf{x})$ by some method, or least to obtain bounds for each component $\nabla^i f_k(\mathbf{x})$ that would allow the proof to go through.

The large increase in analytic complexity caused by the addition of even the simplest interaction term is cause for both consternation and challenge. The results presented here are meant to stimulate some of the challenge.

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7824

RECIPROCAL HYBRIDIZATION BETWEEN THE CALIFORNIA AND GULF OF CALIFORNIA GRUNIONS, *LEURESTHES TENUIS* AND *LEURESTHES SARDINA* (ATHERINIDAE)

The California grunion, *Leuresthes tenuis*, and the Gulf of California grunion, *L. sardina*, are the only fishes that temporarily leave the water during spring high tides to deposit their eggs in beach sand (Walker 1952). The eggs develop in the nearly dry sand and hatch when uncovered and agitated by the surf of the next series of high tides.

The grunions have an allopatric distribution. The California grunion ranges from Monterey Bay, Calif., to Bahía Magdalena, Baja California Sur. The Gulf grunion is endemic to the Gulf of California, ranging from Bahía Concepcíon, Baja California Sur, and Guaymas, Sonora, Mexico to the mouth of the Río Colorado (Moffatt and Thomson 1975).

Recent comparisons show that morphological, physiological, and behavioral differences exist between the grunions. Morphologically very similar, the most diagnostic characterictics distinguishing them are lateral scale row counts; the mean number in *L. tenuis* is 75 and in *L. sardina* is 55. Gulf grunion adults are also significantly longer, more slender, have a smaller eye diameter, and are more lightly pigmented than those of the California grunion (Moffatt 1974; Moffatt and Thomson 1975). Gulf of California grunion have wider embryonic and larval thermal tolerances, a higher larval preferred temperature, and wider larval salinity tolerances (Reynolds and Thomson 1974a, b, c; Reynolds et al. 1976, 1977; Moffatt 1977).

Light response remains positive in Gulf grunion through adulthood, whereas the response shifts from positive in the larvae to negative in the adults of the California grunion (Walker 1952; Reynolds and Thomson 1974c; Reynolds et al. 1977). In response to the shorter wave period in the northern Gulf of California, the duration of the spawning act of the Gulf grunion females is much briefer than that of the California grunion females (Thomson and Muench 1976; Muench 1977).

Only recently has the congeneric status of the grunions been recognized (Moffatt 1974; Moffatt and Thomson 1975). Evidence to date indicates that the California grunion, the less primitive of the two species, has adapted to the less fluctuating tidal and thermal regimes of the California coast, following isolation from an ancestral type by the

Baja California peninsula (Moffatt and Thomson 1975; Moffatt 1977).

Hybridization and hybrid survival experiments have been widely used as indices of divergence and have made valuable contributions as a tool in the definition of phylogenetic relationships (Hubbs 1967, 1970). In an attempt to further illuminate the relationship between the grunions, we made artificial and reciprocal crosses and we report on the first successful reciprocal hybridization of *Leuresthes tenuis* and *L. sardina*.

Materials and Methods

Adult grunions, although easily obtained in large numbers, are difficult to maintain and transport alive. On 18 March 1976 (2330 PST), milt from six California grunion males was collected at Scripps Beach, La Jolla Calif., mixed in the beaten yolks of two hen eggs (Bratanov and Dikov 1961), and transported to El Golfo de Santa Clara, Sonora, Mexico. The milt-yolk mixture, maintained between 16° and 20°C, was used to fertilize the eggs from 8 to 10 Gulf grunion females obtained at El Golfo on the following day (19 March) during a spawning run which began about 1700 MST. During this same run Gulf grunion milt was collected from 6 to 7 males, transported in the same manner and used to fertilize California grunion eggs from about 10 females obtained during a run that night at La Jolla at 0115 PST (20 March). One prior and four subsequent attempts to hybridize the grunions were made during the 1975, 1976, and 1977 spawning seasons, but these were unsuccessful because one or both grunions failed to spawn.

The female grunions were rinsed thoroughly in clean seawater before their eggs were stripped directly into the milt-yolk mixture. The mixture was diluted slightly with fresh seawater to increase sperm motility, gently agitated, and kept cool until the end of the spawning run. The eggs were then strained, rinsed with seawater, and placed in plastic refrigerator containers between moist paper towels for transport and incubation.

Conspecific control embryos of each species were obtained by mixing eggs and milt in a bucket of seawater, one-third full, and did not involve the transportation or preservation of milt in hen yolk. When spawning individuals were plentiful, as at the Gulf grunion run on 19 March, six to nine males were stripped per one female in order to achieve maximum fertilization levels (Moffatt 1977).

Both sets of hybrid fertilized eggs and the conspecific controls of *L. tenuis* (18 March) and *L. sardina* (19 March) were transported from San Diego, Calif., to the University of Arizona at Tucson aboard commercial airlines. Upon arrival (22 h postfertilization in *L. sardina* × *L. tenuis* and *L. sardina* controls; 13 h in *L. tenuis* × *L. sardina;* and 32 h in *L. tenuis* controls) each set of eggs was inspected. Their development was monitored daily thereafter.

Both California grunion spawning runs were sparse at La Jolla. Therefore, the greatest portion of eggs and sperm available were devoted to the hybridization experiments and a low conspecific *L. tenuis* sample size resulted. Consequently, the developmental and hatching data reported herein for these embryos are a compilation of these few controls and egg sets obtained on other occasions, incubated at 20°C from 12 h postfertilization (Moffatt 1977).

Yolk-sac larvae of the two hybrids and the conspecific controls were placed in separate tanks containing artificial seawater and raised on newly hatched *Artemia*, freeze-dried marine zooplankton, commercial staple food, and frozen *Artemia* nauplii. Larvae of the hybrids and controls were maintained for nearly 5 mo although initial mortality rates (first 2 mo) in all groups were high (>90%). On 19 August, 141 days posthatching, the aquaria air lines were fouled by compressor oil and the few remaining hybrids and controls died. Only two *L. tenuis* × *L. sardina* and nine *L. sardina* × *L. tenuis* individuals survived to a size (>12 mm) at which the scale rows could be counted. This is not to imply that scales might not have been present prior to this time, merely that no attempt was made to count them.

Results

At 22 h postfertilization, cleavage had progressed to the gastrula stage in *L. sardina* × *L. tenuis* embryos as it had in the *L. sardina* controls. The *L. tenuis* × *L. sardina* hybrids had reached a 32-cell blastodic stage at 13 h postfertilization as do *L. tenuis* embryos.

Artificial fertilization levels in the conspecific controls fell between 85 and 99% during the peaks of their spawning seasons when male to female ratios of 6 or 9:1 were available. The fertilization levels of both hybrids ranged from 60 to 70%. These diminished levels in the hybrids may have resulted from a combination of several factors such as: the low male to female ratios used (<1:1); decreased sperm motility in the viscous hen-yolk medium; high sperm mortality due to time, starvation, temperature shock, handling, etc. or partial reproductive isolation between the species in the form of mild fertilization block to nonconspecific spermatozoa.

The grunions, *L. tenuis* and *L. sardina*, showed similar developmental rates (Moffatt 1977). Development proceeded normally in the hybrids and at about the same rate as the controls. No unusual embryonic mortality was observed in the hybrids, evidence that these embryos were not gynogenetic hybrids (Moore 1975).

Preliminary trials showed that hen's yolk and seawater alone will not initiate cleavage in Gulf grunion eggs. Precautions were taken to prevent conspecific milt contamination. Preliminary examination of cellular nuclei smears of developing embryos immersed in colchichine revealed somatic chromosome numbers of about 2n = 40 in all four sets of embryos (controls and hybrids), further evidence that these embryos were true diploid hybrids.

Grunion embryos will hatch after vigorous agitation in seawater. On 31 March at 284 h (11.8 days) postfertilization, 65.6% of the *L. sardina* × *L. tenuis* embryos hatched and 66.5% of the *L. tenuis* × *L. sardina* embryos hatched at 272 h (11.4 days). These hatch times are similar to those of the controls. Hatching can be induced in both grunions at 10.2 days postfertilization when embryos are incubated at 20°C (Moffatt 1977).

Newly hatched *L. tenuis* larvae are typically more darkly pigmented; they have a larger eye diameter; they are stronger swimmers; and they are more capable of escaping net capture than newly hatched *L. sardina* larvae (Moffatt 1977). *Leuresthes tenuis* larvae are 10% longer (mean total length = 7.70 mm) than those of *L. sardina* (mean total length = 6.93 mm). The greater length of the California grunion yolk-sac larvae occurs in the postanal region as in the adults. California grunion larvae are also 52% heavier (mean dry weight = 0.340 mg) whereas, the mean dry weight of *L. sardina* equals 0.223 mg (Moffatt 1977). The greater length and weight of the California grunion at hatching may be attributable to the 4.10 times greater ovum volume (Moffatt 1977; Moffatt and Thomson in press).

These differences which distinguish the prolarvae of *L. tenuis* and *L. sardina* were also observed in the hybrids. In most characteristics the *L. tenuis* × *L. sardina* larvae were not visibly distinguishable from the maternal controls (*L. tenuis*), e.g., size, pigmentation, and swimming ability. However, the *L. sardina* × *L. tenuis* larvae appeared to be somewhat intermediate to the controls in extent of pigmentation and swimming ability. At 2 wk after hatching the length and pigment differences between the larvae were more pronounced. Premaxillary teeth were visible in the *L. sardina* × *L. tenuis* larvae but not in the reciprocal hybrids. Again, hybrids closely resembled the maternal controls. Gulf grunion adults typically have much stronger dentition than do the adults of the California grunion (Moffatt and Thomson 1975).

As previously mentioned, the most diagnostic differences between the adult grunions are the lateral scale row counts. Scale counts of the 141-day-old controls were essentially the same as those of the adults (Table 1). The counts of the hybrids were intermediate and significantly different from each other. Those shown by both hybrids were significantly different from those of both parental species. The lateral scale rows of the hybrids were closer in number to those of the maternal controls. Mean counts of *L. sardina* × *L. tenuis* were 32% closer to those of *L. sardina;* and *L. tenuis* × *L. sardina* were 20% closer to *L. tenuis* than to those of the paternal parents, *L. tenuis* and *L. sardina*, respectively.[1] The intermediate counts indicate paternal genome influence and that these are indeed diploid hybrids.

TABLE 1.—Means, ranges, *n*, and *P* values of lateral scale row counts observed in 141-day-old hybrids and controls and adults of the grunions, *Leuresthes tenuis* and *L. sardina*.

Parents	*L. tenuis*			*L. sardina*		
	Juveniles	Adults	*P*	Juveniles	Adults	*P*
L. tenuis	*x* 75.5 (75-76) *n* 2	*x* - 74.6 (69-80) *n* 143	·0.6	*x* 61.8* (61-63) *n* 9	—	—
L. sardina	*x* 67.0* (66-68) *n* 2 *P*· 0.01	— —	—	*x* 55.1 (54-57) *n* 9 *P*· 0.001	*x* 55.3 (51-60) *n* 177 —	·0.7

*Student's *t*-test comparison of the lateral scale row counts between the two hybrids *P*· 0.001

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[1] A mean hybrid count greater or less than 65 (the midvalue between the parental species) indicated the affinity to one parent or the other. The numerical affinities (percentages) were calculated as the ratio of the differences between 65 and the hybrid count and between 65 and the adult counts.

Discussion

Natural hybridizations are reportedly more common among freshwater fishes than among marine fishes (Hubbs 1955). Hubbs (1970) stated that, "teleost hybrids are relatively easily produced and if the parental morphology is similar the hybrids are easily reared." The results of natural and artificial amphibian and teleost crosses have been widely employed for estimating degrees of phylogenetic divergence, revealing systematic patterns, and explaining mechanisms controlling development and differentiation.

Davidson (1968) reports that the closer the phylogenetic relationship between the species hybridized, the less likely the hybrid genome control will be displayed early in development. This is because the mechanical aspects of early development tend to be similar in closely related species and may be primarily under the control of maternal RNA accumulated in the egg prior to fertilization. Davidson believes this, at least in part, accounts for the commonly observed resemblance of hybrids in early developmental stages to the maternal parent. The genetic influence of the paternal genes in the hybrid genome may not be apparent phenotypically until long after the onset of differentiation (Davidson 1968).

It is possible that such mechanisms account for the maternal resemblance pattern observed in the grunion hybrids as well. The hybrids resembled the maternal parents in overall size and body proportions, coloration, swimming ability, net-escape capability, and dentition until long after hatching. Only when the lateral scale rows were counted at 141 days after hatching did the influence of paternal genes become visibly and quantitatively apparent.

The numerous artificial and two natural hybridizations (interspecific and intergeneric) reported among the Atherinidae are reviewed by Hubbs and Drewry (1959), Rubinoff (1961), and Hubbs (1970). Natural hybrids reported between *Menidia menidia* and *M. beryllina* along the Atlantic coast of Florida (Gosline 1948) exhibit intermediate counts (i.e., scales and fin rays). Most of the experimental crosses between these atherinids resulted in low developmental success and low survival rates except those of *M. beryllina* ♀ × *M. menidia* ♂ (Rubinoff 1961). Rubinoff did not report whether any intermediate characteristics existed in these hybrids nor was the reciprocal cross attempted.

Geographically isolated species forms adapt to their respective environments by the evolution of appropriate gene complexes. Then, if sympatry reccurs and hybridization takes place, hybrid individuals will usually be selected against (Mayr 1963; Ford 1964). Hybrids not selected against will usually be successful over only a narrow geographical range, since in animals, natural hybridization is commonly associated with environmental perturbation (Mayr 1963; Manwell and Baker 1970).

The *Menidia* species are sympatric and hybridization does occur in northern Florida, a very narrow portion of the overlap in their ranges (Gosline 1948). Like these species, grunions are marine fishes with similar, but not identical, ecological preferences. However, the grunions are allopatric and natural hybridization is not possible.

According to Mayr (1963), some investigators argue that renewed sympatry with hybridization is required as a process of speciation in order to "perfect isolating mechanisms," and, therefore, unlike the *Menidia* species, the heterospecific status of the grunions may be questioned, especially in light of the hybridization success reported herein. We conclude that, despite our success at hybridizing *L. tenuis* and *L. sardina,* the morphological, physiological, and behavioral distinctions between them warrant their continued recognition as separate species.

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NANCY M. MOFFATT

Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 271, La Jolla, CA 92038

DONALD A. THOMSON

Department of Ecology and Evolutionary Biology
University of Arizona
Tucson, AZ 85721

TYCHOPLANKTONIC BLOODWORM, *GLYCERA DIBRANCHIATA*, IN SULLIVAN HARBOR, MAINE

The bloodworm, *Glycera dibranchiata*, is distributed from the Gulf of St. Lawrence to the Gulf of Mexico and from central California to lower California and Mexico. It occurs from intertidal water to 402 m depth (Pettibone 1963), but it is more abundant in shallow coastal water. In Maine and Nova Scotia the worms are dug commercially along the coast from the upper layers of the intertidal sand-silt-clay strata (Dow and Creaser 1970; Anonymous 1974; Glidden[1]).

Spawning bloodworms are briefly pelagic occurring in large numbers as they swarm in the afternoon. Creaser (1973) observed swarming in Maine during June. Simpson (1962) reported swarming both in June and November-December, suggesting a biannual spawning in Maryland. Klawe and Dickie (1957) did not observe swarming by bloodworms in Nova Scotia, although other evidence indicated that the worms spawned in mid-May. They suggested that the worms had a short nocturnal swarming period making them difficult to observe. Simpson (1962) checked this possibility

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[1] Glidden, P. E. 1951. Three commercially important polychaete marine worms from Maine: *Nereis (Neanthes) virens*, *Glycera dibranchiata*, *Glycera americana*. Rep. to Maine Dep. Sea Shore Fish., Augusta, Maine.

7825

Larvae and Pelagic Juveniles of Blackgill Rockfish, *Sebastes melanostomus*, Taken in Midwater Trawls off Southern California and Baja California

H. GEOFFREY MOSER AND ELBERT H. AHLSTROM

National Oceanic and Atmospheric Administration, National Marine Fisheries Service,
Southwest Fisheries Center, La Jolla, Calif. 92038, USA

MOSER, H. G., AND E. H. AHLSTROM. 1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35: 981–996.

Examination of 217 midwater trawl samples from the coastal basins off southern California and Baja California revealed a recurring group of rockfish species. The late larvae and pelagic juveniles of the blackgill rockfish, *Sebastes melanostomus*, constituted 16% of the total number of rockfish specimens. The life-history stages of this species are described, with emphasis on the pelagic juvenile stage. Late stage larvae and pelagic juveniles develop a distinctive pattern of melanophore bands which, by disrupting the body outline, may help conceal the young during their midwater existence. Evidence from midwater trawl collections suggests that 30-mm pelagic juveniles migrate or are carried shoreward at a depth of ~200 m to the appropriate habitat for settling. The high relative abundance of blackgill rockfish pelagic juveniles in midwater trawl samples suggests that this species may represent a potential resource.

Key words: blackgill rockfish, *Sebastes melanostomus*, larvae, pelagic juveniles, midwater trawls, developmental stages, melanophore patterns, life-history strategy, head-spine development

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L'examen de 217 échantillons prélevés au chalut mésopélagique dans les bassins côtiers au large de la Basse-Californie et du sud de la Californie a permis de mettre en évidence la réapparition d'une espèce de sébaste dans cette région. Des stades larvaires avancés et des juvéniles pélagiques de *Sebastes melanostomus* constituaient 16% du nombre total de spécimens de sébastes. Nous décrivons les stades du cycle biologique de cette espèce, en mettant l'accent sur le stade juvénile pélagique distinctif. Le stade larvaire avancé et les juvéniles pélagiques se distinguent par leurs bandes de mélanophores qui, en brisant le contour du corps, peuvent contribuer à dissimuler les jeunes durant leur vie pélagique. Certaines données recueillies grâce au chalut portent à croire que les juvéniles pélagiques de 30 mm migrent vers le rivage ou y sont transportés jusqu'à une profondeur d'environ 200 m, où ils trouvent leur habitat définitif. L'abondance relative élevée des juvéniles pélagiques de *Sebastes melanostomus* dans les échantillons de chaluts mésopélagiques porte à croire que cette espèce pourrait représenter une ressource exploitable.

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IN recent years the rockfishes, now referred to the genus *Sebastes*, have become increasingly important as a commercial and recreational resource in coastal waters from Mexico to Alaska. In California, for example, rockfishes increased from 29 to 71% of the party-boat catch during the 10-y period from 1965 to 1974 (McAllister, 1976). During this same period the commercial landings of rockfishes in California more than doubled and increased fivefold in value (Greenhood and Mackett 1967; McAllister 1976). Along the entire Pacific coast commercial landings of rockfishes, excluding *Sebastes alutus*, increased from 18.8 to 28.9 million pounds (8535 to 13 120 tonnes (t)) over the same period (Verhoeven 1976).

The Pacific ocean perch (*S. alutus*) has presented a striking example of overexploitation. Until 1960, the northeastern Pacific stocks of this species were fished only by United States and Canadian trawlers, who took fewer than 5000 t annually and only fished in the southernmost portion of the range of commercially abundant stocks (southern Oregon to central British Columbia). By 1965, however, the Russians and Japanese, who had entered the fishery in 1960 off

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Alaska, had expanded their fishery southward to southern Oregon. In 1965 their total catch peaked at 520 000 t (Chikuni 1975). Thereafter the fishery declined rapidly and stabilized at about one-fourth that of the peak catch. The overexploitation of *S. alutus* demonstrates the need for effective management of other rockfish species, which are subjected to increased fishing pressure. The problem is complicated by the large species complement (about 70), difficulties in identification, and inadequate knowledge of the life histories of many species.

Sampling the planktonic larvae of *Sebastes* is one of the potential means of estimating year-class abundance at an early age; however, the early developmental stages are known for only a few species (Moser et al. 1977). At the end of the larval period the species of *Sebastes* follow divergent strategies. Some, like *S. paucispinis*, move to inshore nursery areas such as eelgrass beds (Moser 1967). Others, like *S. diploproa* and *S. rubrivinctus*, spend their early juvenile life in masses of floating kelp and flotsam (Mitchell and Hunter 1970; Boehlert 1977). Still others, such as *S. macdonaldi*, have an extended pelagic juvenile stage (Moser 1972).

A study of the *Sebastes* larvae and juveniles taken by midwater trawl in the deep-water basins off southern California and Baja California revealed a recurring group of a few common types. One of these, the blackgill rockfish (*S. melanostomus*), has a striking pigment pattern and could be assembled into a continuous developmental series from 6.2 to 46.2 mm. In this paper we describe this series and point out the potential of using the pelagic juvenile stages of certain species of *Sebastes* in resource assessment.

Materials and Methods

A total of 217 midwater trawl collections containing *Sebastes* larvae and juveniles was examined; of these, 202 were provided by the Los Angeles County Museum of Natural History, 6 by the Scripps Institution of Oceanography (SIO) Fish Collection, and 9 by the National Marine Fisheries Service, La Jolla. Of the Los Angeles County Museum collections all but 20 were made with an open 10-ft (3-m) Isaacs-Kid midwater trawl. Two were made with an open 30-ft (9-m) midwater trawl, 1 was made with a 6-ft (1.8-m) ring net, and 17 were discrete depth samples made with an acoustically operated 6-ft (1.8-m) Tucker opening–closing net. The open midwater trawls were fished horizontally at maximum depth for 2 h. Maximum depths ranged from 10 to 1350 m (Table 1) over a range of bottom depths of 210–4389 m ($\bar{x} = 2225 \pm 973$ SD). Depths sampled by the opening-and-closing nets are listed in Table 1.

A total of 1310 larvae and juveniles of *Sebastes* was examined of which 211 (16%) represented *S. melanostomus* (Table 2). The distribution and size frequency of *S. melanostomus* are shown in Fig. 1 and 2. Newborn larvae obtained from a pregnant female of this species, caught on March 13, 1975 and identified with the characters of Barsukov (1968), Tsuyuki and Westrheim (1970), and Miller and Lea (1972), were raised to the point of yolk depletion. These larvae helped confirm the identification of the trawl-caught series and were used in the description of the larvae. The descriptive methods follow those of Moser et al. (1977). Terminology of the head spines follows that of Eschmeyer (1969), Moser (1972), and Poss (1974).

TABLE 1. Maximum depths (m) of midwater trawls used in this study (Los Angeles County Museum material).

Open trawls				Discrete depth trawls	
Depth range	No. of tows	Depth range	No. of tows	Depth	No. of tows
0–50	25	601–650	5	200	6
51–100	31	651–700	11	225	1
101–150	7	701–750	1	250	1
151–200	4	751–800	3	300	1
201–250	8	851–900	7	350	3
251–300	5	901–950	6	450	1
301–350	25	951–1000	1	525	1
351–400	4	1051–1100	4	550	1
401–450	7	1151–1200	6	650	1
451–500	6	1251–1300	10	800	1
501–550	3	1301–1350	1		
551–600	4	Unknown	1		

TABLE 2. Composition of *Sebastes* identified in midwater trawl samples from southern and Baja California.

Sebastes type	No. of specimens	% total
S. aurora	16	1
S. diploproa (juveniles)	25	2
S. levis	2	<1
S. macdonaldi	4	<1
S. melanostomus	211	16
S. paucispinis	6	<1
S. rubrivinctus	51	4
Subgenus *Sebastomus*	585	45
S. spp.	410	31
Total	1310	

The terminology of specimen length requires special explanation. Standard length is defined as the distance between the tip of the snout and the posterior edge of the hypural plate. In larvae that have not completed notochord flexion, and therefore do not have the posterior edge of the hypural plate in a vertical position, we measure the body length from the tip of snout to the tip of the notochord. Notochord flexion in *S. melanostomus* is completed at a length of 7.5 mm and specimen length in larvae larger than this is referred to as standard length.

Fresh specimens for aging were obtained from the stomach contents of albacore (*Thunnus alalunga*) taken in August 1977 about 80 miles (129 km) south–southwest of San Diego, Calif. The otoliths were prepared and analyzed according to the methods of Brothers et al. (1976).

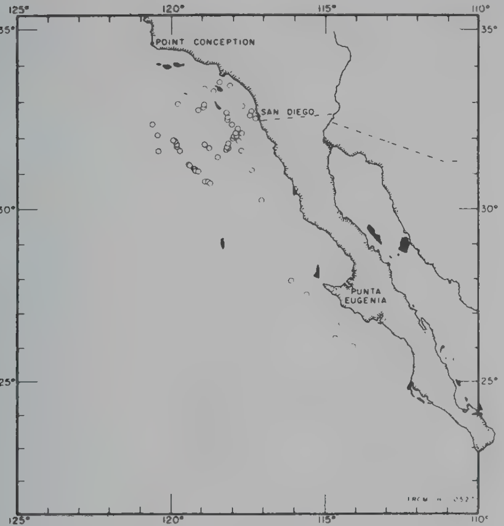


FIG. 1. Distribution of midwater trawl samples containing larvae and pelagic juveniles of *Sebastes melanostomus*.

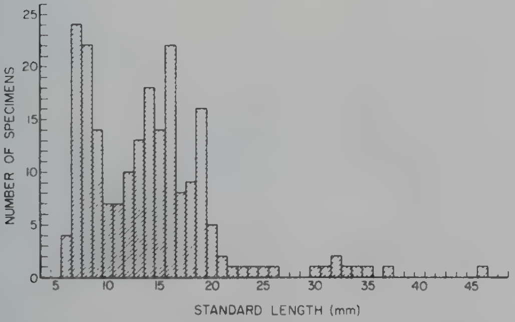


FIG. 2. Length frequency of total midwater trawl catches of *S. melanostomus* taken off southern and Baja California.

Results and Discussion

DISTINGUISHING FEATURES

Larvae of *S. melanostomus* are extruded at a length of about 4.5 mm. Although there is a gap in our series between 4.5 and 6.2 mm (Table 3), some of the pigment present on the smallest trawl-caught specimens is also evident on newborn larvae. Newborn larvae have a single row of melanophores (mean of 8 melanophores for 27 specimens counted) on the ventral midline of the tail, a patch above the brain, a heavy blotch at the tip of the lower jaw, a streak along the posterior region of the upper jaw, a pattern of minute melanophores on the pectoral fins, and a group along the dorsal and lateral surfaces of the gut (Fig. 3). A large blotch that appears on the opercle at about the completion of notochord flexion, along with the upper jaw streak that has moved anteriad, helps to distinguish larvae of this size. Older larvae and pelagic juveniles develop a striking banding, which is retained in benthic juveniles and even to some extent in adults (Fig. 3–5). Larvae and pelagic juveniles develop unusually prominent head spination. The beginning of the pelagic juvenile stage is marked by the appearance of anterior lateral-line scales in 16.0-mm specimens. The largest pelagic juvenile examined measures 46.2 mm, and the smallest demersal juvenile 36.0 mm.

MORPHOLOGY

Body proportions for larvae and pelagic juveniles of *S. melanostomus* and of four other species of *Sebastes* studied previously (Moser et al. 1977) are listed in Table 4. Larvae and pelagic juveniles of *S. melanostomus* are comparatively deep-bodied, big-headed, and have eyes of moderate size. Relative head length is considerably greater in flexion-stage larvae of *S. melanostomus* than in the other species.

The development of prominent head spines is the outstanding morphological feature of *S. melanostomus* larvae. The sequence of development of head spines in early larvae of *Sebastes* has been described for *S. macdonaldi* (Moser 1972). The more complete series of late-stage larvae and pelagic juveniles of *S. melanostomus* provides an opportunity to describe the development of these spines in greater detail. Their development and eventual fate is described in relation to the bones that bear them in the approximate sequence of their appearance (Table 5, Fig. 6 and 7).

Parietal — Parietal bones bear serrated ridges that terminate in prominent spines. Posterior to each parietal spine is a nuchal spine. Initially the nuchals are small and subjacent to the parietals; however, during larval development the nuchals enlarge in relation to the parietals and eventually equal them in size (Fig. 7B). Both spines are retained in adults.

Frontal — The frontal bone, which forms a shelf above the eye, eventually bears two spines. Initially the postocular spine forms directly above the eye but gradually moves posteriad with development to assume a rearward position above the orbit at the end of pelagic life. The second spine to develop on the shelf is the supraocular. Initially it is located forward but moves posteriad with development to a position above the center of the orbit. Supraocular and postocular spines are retained in adults. At the beginning of the pelagic juvenile stage the tympanic spine begins to form on the upper rim of a sensory-canal opening. The spine enlarges to eventually obscure the opening at the end of pelagic life. On the largest stained pelagic juvenile examined a single coronal spine is present on the right side

TABLE 3. Measurements (mm) of larvae of *Sebastes melanostomus*. Specimens between dashed lines are undergoing notochord flexion and those between solid lines are pelagic juveniles.

Specimen length	Snout–anus distance	Head length	Snout length	Eye diam	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout–anal fin interval
4.5	1.7	0.96	0.28	0.36×0.39	1.0	0.25	0.23		
6.2	3.7	3.0	1.0	0.92×0.96	2.2	1.2	0.79	0.64	4.0
6.8	3.8	3.4	1.0	1.0×1.1	2.4	1.3	0.80	0.77	4.2
7.2	3.8	3.2	1.0	1.0×1.1	2.5	1.3	0.84	—	4.3
7.6	4.4	3.4	1.2	1.1×1.1	2.9	1.8	0.87	1.1	4.8
7.8	4.7	3.4	1.2	1.1×1.1	3.0	1.6	0.90	1.0	4.9
8.2	4.5	3.2	1.0	1.2×1.2	3.4	1.6	1.0	1.2	5.1
8.5	4.8	3.7	1.2	1.2×1.2	3.2	1.9	1.0	1.3	5.2
9.0	5.2	3.8	1.2	1.2×1.2	3.4	1.9	1.2	1.3	5.4
10.1	5.8	4.0	1.2	1.4×1.4	4.2	2.2	1.2	1.5	6.1
11.3	6.7	4.7	1.4	1.6×1.6	4.4	2.6	1.2	1.8	6.8
12.3	7.6	5.0	1.6	1.7×1.7	4.5	2.6	1.3	2.0	8.2
13.5	8.0	5.2	1.6	1.8×1.8	5.2	2.9	1.3	2.2	8.6
14.5	9.1	5.7	1.9	1.9×1.9	5.6	3.1	1.4	2.4	9.8
15.7	9.7	6.2	1.8	2.0×1.9	5.9	3.6	1.6	3.1	10.1
16.2	9.8	6.5	2.2	2.1×2.0	6.2	3.5	1.5	3.1	10.3
17.4	10.6	6.2	1.9	2.2×2.2	6.5	5.0	1.7	3.3	11.0
18.6	11.5	7.2	2.3	2.3×2.2	6.7	4.4	1.8	3.5	12.3
19.8	12.7	7.9	2.7	2.3×2.3	7.2	4.7	1.8	3.8	13.4
20.7	13.0	8.0	2.7	2.4×2.4	8.0	5.2	2.1	4.2	13.5
21.4	13.2	7.8	2.2	2.5×2.5	8.5	5.7	2.2	4.0	13.7
23.3	14.5	8.6	2.4	2.7×2.7	8.7	6.2	2.3	4.8	15.4
24.0	16.6	10.1	2.8	2.8×2.8	9.0	6.2	2.3	—	16.9
25.2	16.7	10.1	—	3.0×3.0	9.2	6.2	2.3	4.9	17.2
26.4	16.9	10.0	2.9	2.9×2.9	9.9	6.9	2.7	5.2	17.7
30.1	19.6	12.0	3.2	3.3×3.3	10.3	8.1	2.7	6.0	19.5
32.7	20.7	12.7	3.3	3.2×3.2	12.0	8.8	3.0	6.7	21.7
33.5	23.3	13.2	3.3	4.2×4.2	12.7	9.1	3.3	7.1	24.4
34.5	21.6	13.2	3.6	3.8×3.8	11.8	9.3	3.3	6.9	22.7
37.2	24.3	14.0	3.5	4.1×4.1	12.5	10.1	3.3	7.0	25.5
46.2	29.5	15.7	4.2	4.7×4.7	17.2	13.0	4.4	9.5	31.1
36.0[a]	22.5	12.8	2.7	4.0×4.0	13.7	10.1	3.4	7.5	24.7
42.1[a]	27.2	15.7	4.8	4.3×4.3	14.7	11.3	3.8	8.8	29.0
60.6[a]	37.9	22.0	5.2	7.5×7.5	21.4	16.9	5.8	11.8	41.1

[a] Benthic juvenile.

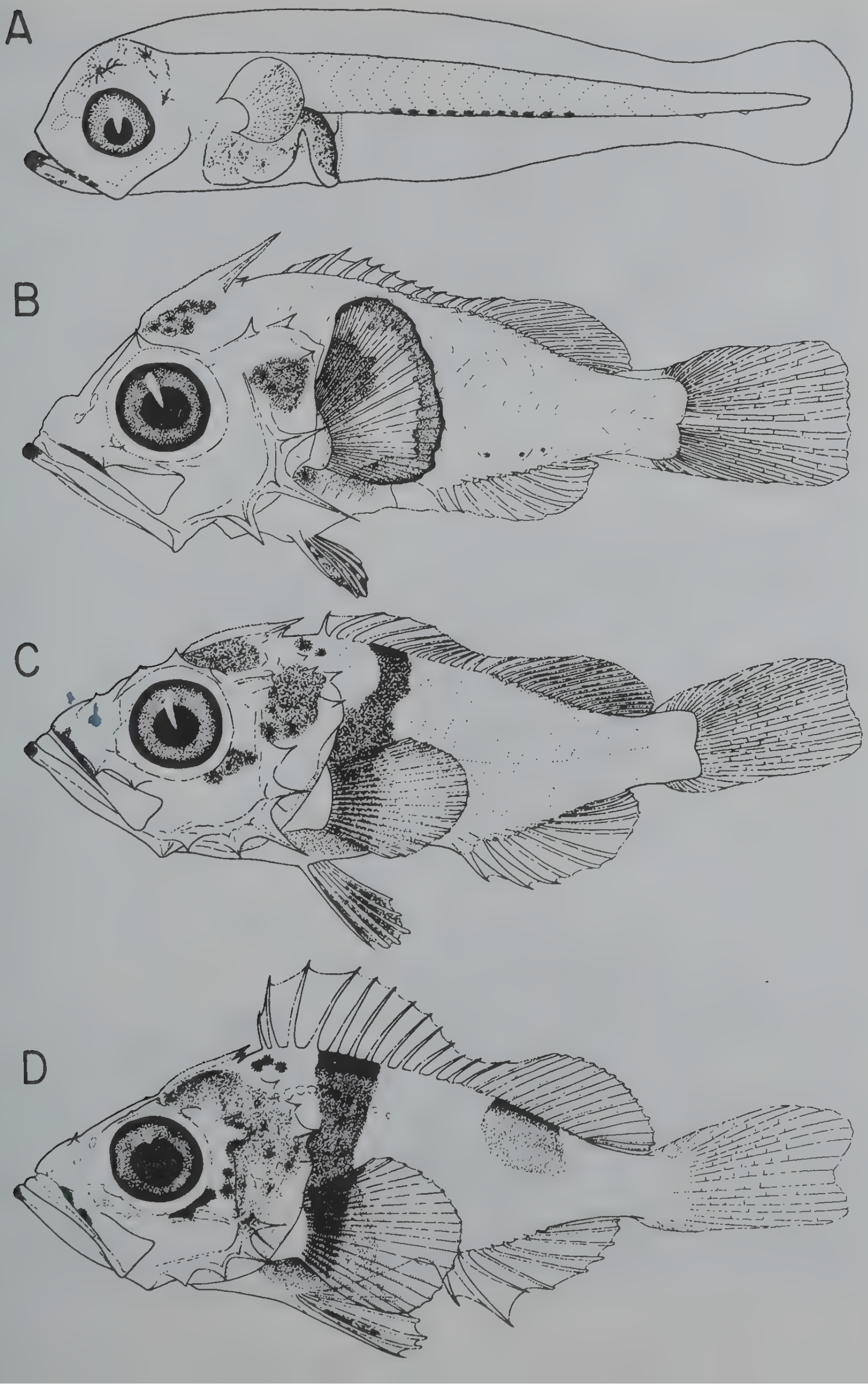
of the interorbital region. They are present on no other pelagic juveniles in our collection and are only occasionally reported in adults.

Pterotic — The large spine on the pterotic bone forms early in the larval period and remains prominent until it disappears at the end of pelagic life.

Preopercle — The spines on the preopercle form early and become highly conspicuous. Two series are formed: a posterior series of large backward-projecting spines and an anterior series of small laterally projecting spines. In the smallest stained larva the 2nd, 3rd, and 4th spines of the posterior series have already developed, and each bears in the anterior series a small spine projecting outward from its base. The 3rd posterior spine is the largest in the series and remains so until the end of the pelagic phase. The 3rd and 4th posterior spines are both serrated. The 1st and 5th posterior spines begin to form in the 6.8-mm larva and with continued enlargement during larval development become equal in size to the others. All five spines in the posterior preopercular series are retained in adults.

The spines in the anterior series do not persist. The

FIG. 3. Developmental series of *S. melanostomus*. A, 4.4-mm larva reared from pregnant female; B, 8.2-mm larva; C, 12.3-mm larva; D, 17.4-mm pelagic juvenile.


A
B
C
D

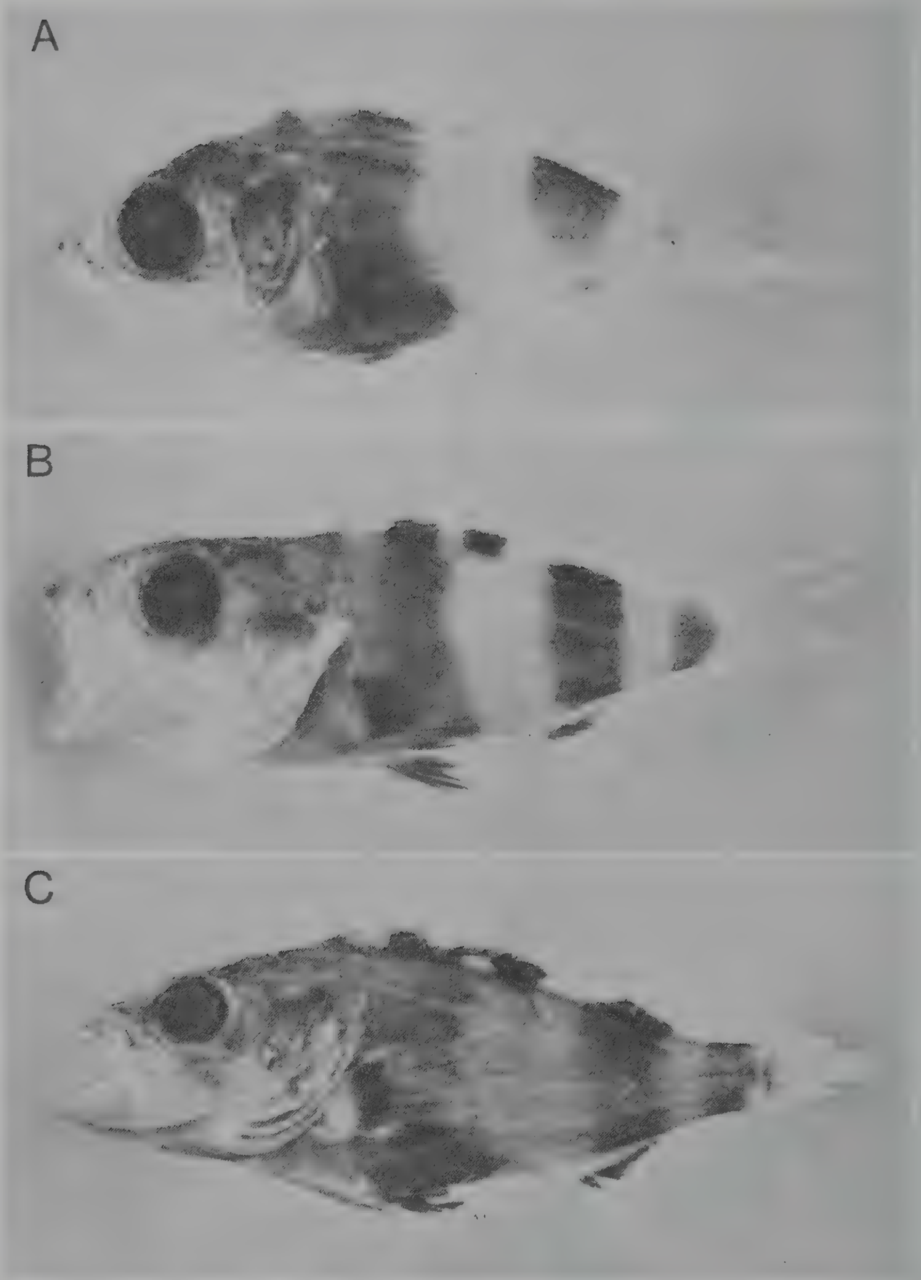


FIG. 4. Pelagic juveniles of *S. melanostomus*. A, 26.4 mm; B, 31.5 mm; C, 46.2 mm.

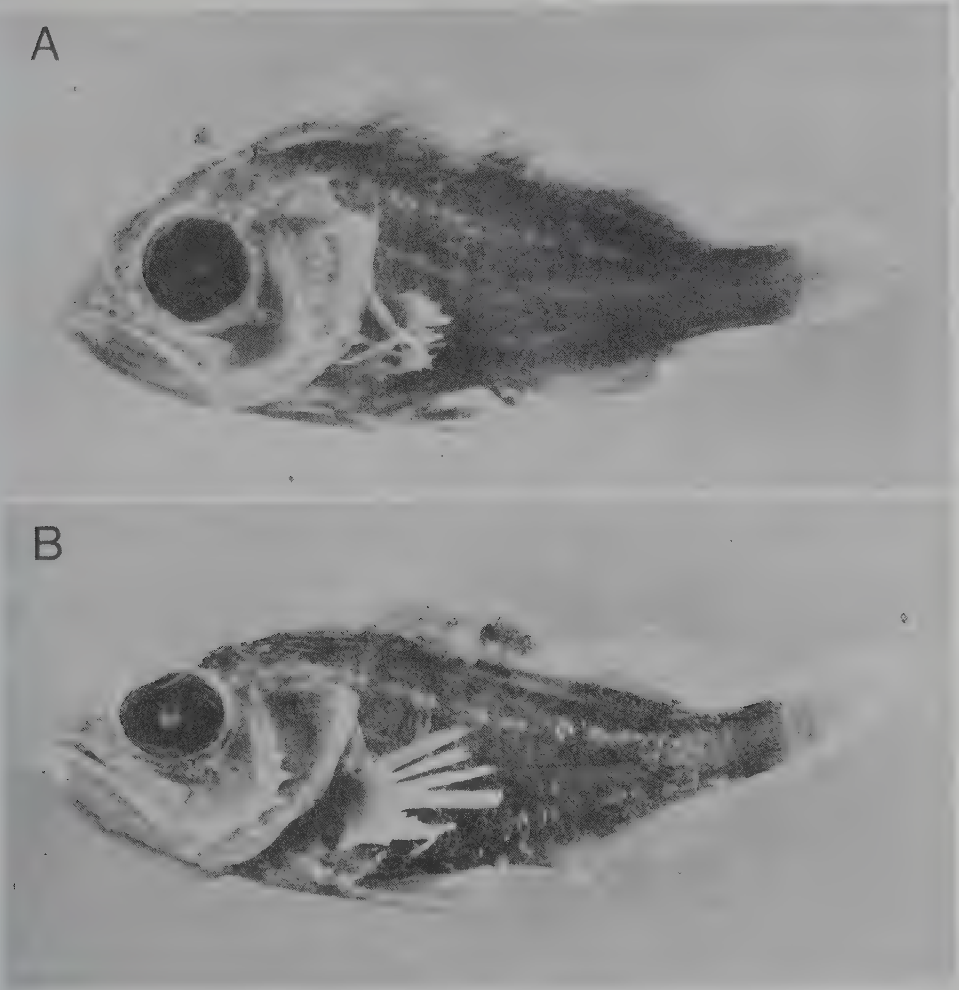


FIG. 5. Benthic juveniles of *S. melanostomus*. A, 36.0 mm; B, 42.1 mm.

one at the base of the 3rd spine of the posterior series is weakly developed or variously lacking on one or both sides until 13.5 mm, after which it is never evident. The ones at the bases of the 2nd and 4th posterior spines gradually diminish in size and are absent in individuals larger than 20.3 mm.

Opercle — A prominent spine is present on the upper posterior edge of the opercle in the smallest stained larva. This upper opercular spine has a long rod-like support that slants ventroposteriad from its point. A second opercular spine with a weaker and shorter supporting rod develops ventral to the former at about 8.8 mm. Upper and lower opercular spines are retained in adults.

Infraorbitals — Confusion and inconsistency mark the nomenclature of the series of bones that underlie the orbit of scorpaeniform fishes. Poss (1974) reviewed the historical aspects of this problem and suggested a rational terminology that we adopt here. The most anterior bone in the series, usually called the lacrymal bone by recent workers, is referred to as infraorbital 1. The next bone posterior to it, usually referred to as suborbital 1, is here termed infraorbital 2. Posterior to it the bone that bears the projection extending to the

TABLE 4. Comparative morphometry of five species of *Sebastes* (A = larvae undergoing notochord flexion, B = postflexion larvae, C = pelagic juveniles). Values given for each body proportion expressed as percentage of body length or head length: mean, standard deviation, and range.

	Snout–anus distance	Head length	Snout length	Eye diam	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length
	Body length	Body length	Head length	Head length	Body length	Body length	Body length	Body length
S. jordani								
A	42.4 ± 1.67 (41–45)	28.4 ± 2.19 (26–30)	35.5 ± 1.29 (34–37)	32.2 ± 2.50 (29–35)	21.0 ± 1.00 (20–22)	8.4 ± 1.14 (7–10)	7.8 ± 0.45 (7–8)	1.4 ± 0.55 (1–2)
B	51.0 ± 2.86 (46–54)	32.3 ± 1.44 (31–36)	34.4 ± 1.98 (31–39)	29.3 ± 2.10 (27–34)	23.8 ± 1.19 (22–26)	16.8 ± 3.25 (11–20)	7.9 ± 1.0 (7–10)	9.0 ± 3.62 (3–13)
C	53.3 ± 1.03 (52–55)	31.2 ± 1.94 (28–33)	34.0 ± 2.83 (30–38)	26.5 ± 1.52 (24–28)	22.2 ± 0.84 (21–23)	20.5 ± 1.05 (19–22)	7.0 ± 0.00 (7)	13.5 ± 1.22 (12–15)
S. levis								
A	48.9 ± 3.44 (45–56)	30.5 ± 1.85 (28–33)	34.8 ± 0.89 (34–36)	32.5 ± 1.77 (30–35)	28.5 ± 3.51 (24–35)	34.9 ± 6.96 (24–46)	12.9 ± 0.64 (12–14)	6.1 ± 3.27 (2–12)
B	59.2 ± 2.87 (57–63)	35.0 ± 2.00 (34–38)	30.2 ± 2.22 (28–33)	30.5 ± 1.73 (28–32)	34.0 ± 1.41 (33–36)	45.0 ± 3.74 (41–50)	11.2 ± 0.96 (10–12)	21.0 ± 4.76 (16–26)
C	63.0 ± 0.82 (62–64)	33.8 ± 0.96 (33–35)	30.5 ± 2.38 (28–33)	27.0 ± 3.37 (25–32)	35.0 ± 1.41 (34–37)	40.8 ± 7.09 (32–47)	10.2 ± 0.96 (9–11)	24.2 ± 2.87 (22–28)
S. macdonaldi								
A	51.8 ± 3.56 (48–56)	35.6 ± 1.52 (34–38)	34.0 ± 4.00 (30–38)	32[illegible] ± 1.41 (31–34)	31.6 ± 2.07 (30–35)	13.0 ± 1.22 (12–15)	—	5.8 ± 2.39 (3–9)
B	60.3 ± 3.06 (55–64)	37.5 ± 1.84 (34–41)	32.9 ± 3.00 (29–37)	33.0 ± 1.33 (31–35)	34.4 ± 1.17 (33–36)	19.3 ± 3.65 (15–26)	—	14.3 ± 3.77 (10–21)
C	64.2 ± 2.44 (61–68)	35.11 ± 2.37 (32–38)	27.9 ± 2.09 (25–32)	30.7 ± 2.74 (26–34)	31.4 ± 1.59 (30–34)	30.4 ± 1.74 (28–34)	—	21.9 ± 1.36 (21–25)
S. melanostomus								
A	56.6 ± 2.99 (53–60)	46.8 ± 2.75 (44–50)	32.0 ± 2.58 (29–35)	32.5 ± 1.00 (32–34)	35.8 ± 1.50 (35–38)	20.0 ± 2.71 (18–24)	12.0 ± 0.82 (11–13)	11.7 ± 2.08 (10–14)
B	59.1 ± 2.69 (55–63)	40.9 ± 2.02 (39–44)	31.5 ± 1.72 (29–35)	33.6 ± 2.07 (31–38)	38.9 ± 1.52 (37–42)	21.5 ± 0.97 (20–23)	11.3 ± 1.06 (10–13)	15.7 ± 1.89 (13–20)
C	63.9 ± 2.67 (60–70)	38.4 ± 1.97 (36–42)	29.0 ± 3.21 (25–34)	30.1 ± 2.29 (25–35)	36.9 ± 1.75 (34–40)	26.1 ± 1.75 (22–29)	9.6 ± 0.50 (9–10)	19.7 ± 0.80 (19–21)
S. paucispinis								
A	44.8 ± 3.70 (40–49)	29.6 ± 1.95 (27–32)	30.6 ± 1.82 (29–33)	30.2 ± 1.64 (29–33)	23.0 ± 1.41 (21–24)	27.2 ± 2.49 (25–31)	9.0 ± 0.71 (8–10)	13.6 ± 9.29 (9–26)
B	57.3 ± 3.82 (51–61)	37.1 ± 1.07 (36–39)	32.2 ± 0.98 (31–33)	31.3 ± 1.70 (28–33)	29.6 ± 0.98 (28–31)	35.7 ± 1.25 (34–37)	7.6 ± 0.53 (7–8)	35.1 ± 2.79 (31–39)
C	62.3 ± 2.73 (60–66)	36.2 ± 1.72 (33–38)	30.5 ± 2.95 (26–33)	27.8 ± 1.72 (26–30)	27.3 ± 0.52 (27–28)	28.2 ± 3.4 (25–34)	6.0 ± 0.89 (5–7)	25.2 ± 2.71 (22–30)

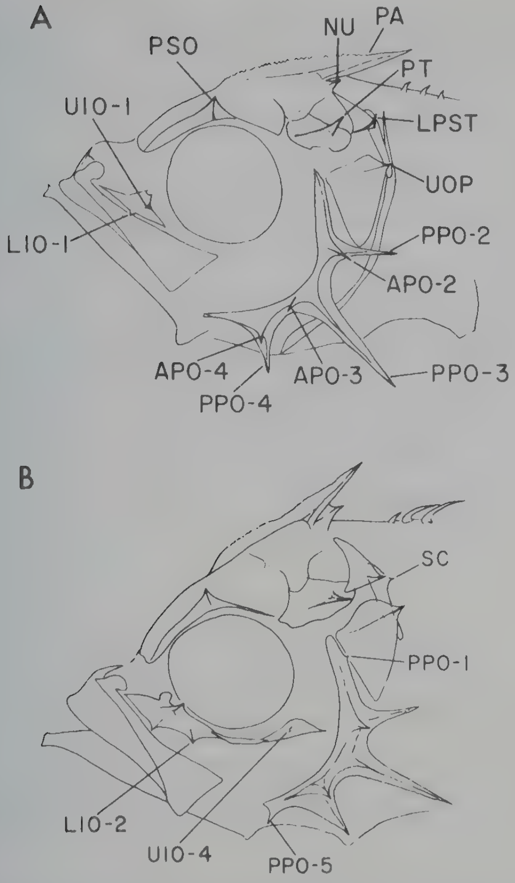


FIG. 6. Head spines in 6.2 mm (A) and 8.2 mm (B) stained larvae of *S. melanostomus.* Abbreviations of head spines: APO-2, 2nd anterior preopercular; APO-3, 3rd anterior preopercular; APO-4, 4th anterior preopercular; CL, cleithral; IOP, interopercular; LIO-1, 1st lower infraorbital; LIO-2, 2nd lower infraorbital; LOP, lower opercular; LPST, lower posttemporal; NA, nasal; NU, nuchal; PA, parietal; PPO-1, 1st posterior preopercular; PPO-2, 2nd posterior preopercular; PPO-3, 3rd posterior preopercular; PPO-4, 4th posterior preopercular; PPO-5, 5th posterior preopercular; PRO, preocular; PSO, postocular; PT, pterotic; SC, supracleithral; SPO, supraocular; TM, tympanic; UIO-1, 1st upper infraorbital; UIO-2, 2nd upper infraorbital; UIO-3, 3rd upper infraorbital; UIO-4, 4th upper infraorbital; UOP, upper opercular; UPST, upper posttemporal.

preopercle and has usually been referred to as suborbital 2 is termed the infraorbital 3.

All three bones develop spines in larvae of *Sebastes.* In our smallest stained larva of *S. melanostomus*, infraorbital 1 bears an outward-projecting spine on its upper edge and a downward-projecting one on its ventral edge. At 8.2 mm a second spine appears posteriorly on the ventral edge of the bone, and at 9.0 mm a second outward-projecting spine forms posterior to the one on the upper edge of the bone. The two upper spines develop as projections on a serrated shelf below the orbit. They become progressively reduced during pelagic life and are obsolete in benthic juveniles and adults. The two lower spines progressively enlarge with development, becoming prominent in juveniles and adults. A single outward-projecting spine develops on the upper lateral face of infraorbital 3 at 7.2 mm. As development proceeds the spine projects from a serrated shelf that rims the orbit. The spine is reduced toward the end of pelagic life and is lost in benthic juveniles. The last spine to appear in the infraorbital series projects outward from the upper edge of infraorbital 2. With development it becomes a projection of the serrated shelf below the orbit, but remains inconspicuous and disappears at the end of the pelagic period.

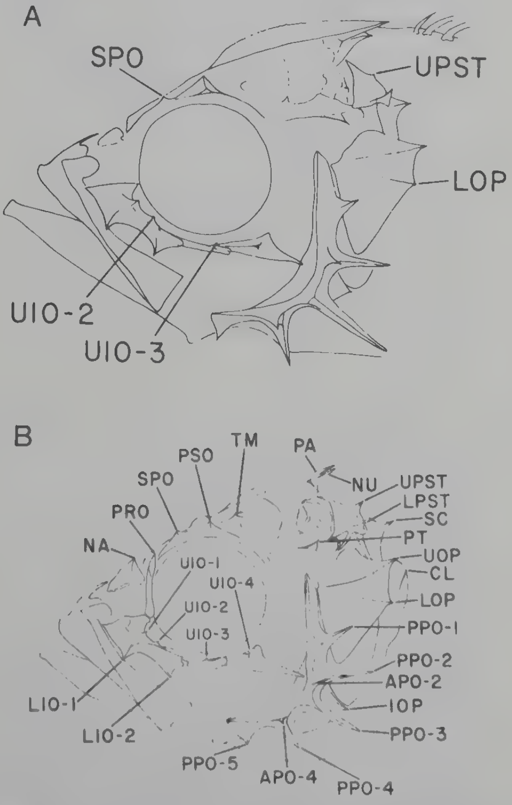


FIG. 7. Head spines in 10.0 mm (A) and 16.0 mm (B) stained larvae of *S. melanostomus.* Abbreviations as in Fig. 6.

TABLE 5. Sequence of development of head spines of *S. melanostomus*. Presence of spine is indicated by an "X" or continuous line. Absence of a spine is indicated by an "O". In asymmetrical specimens the condition on the left and right sides is separated by a slash.

	Length of specimen (mm)																																
Spine	6.2	6.8	7.2	7.5	7.7	8.2	8.8	9.0	9.4	10.0	10.6	11.8	12.0	12.8	13.2	13.5	13.8	14.2	14.7	15.2	15.7	16.0	16.9	17.1	17.7	18.4	18.9	19.5	20.3	21.1	22.4	26.9	32.2
Parietal	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nuchal	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Postocular	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pterotic	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower post-temporal	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Upper opercular	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1st upper infraorbital	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	O
1st lower infraorbital	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2nd anterior preopercular	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X/O	X	X	O	O	O	O
2nd posterior preopercular	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3rd anterior preopercular	X/O	X	O	O/X	X/O	O	O	O	O	O/X	O	O	O	X	O/X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
3rd posterior preopercular	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4th anterior preopercular	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	O	O	O	O
4th posterior preopercular	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1st posterior preopercular		X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5th posterior preopercular		X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4th upper infraorbital			X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Supracleithral						X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2nd lower infraorbital						X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower opercular							X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2nd upper infraorbital								X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	O
Upper post-temporal										X	O	O	X	O/X	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Supraocular										X	O	O	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3rd upper infraorbital										X	O	O	O/X	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	O/X	X	—
Nasal													X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Preocular															X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cleithral																			X	O	O	X	—	—	—	—	—	—	—	—	—	—	—
Interopercular																					X	—	—	—	—	—	—	—	—	—	—	—	—
Tympanic																						X	—	—	—	—	—	—	—	—	—	—	—
Subopercular																								X	O	O	O/X	O	O	O/X	O/X	X/O	X
Coronal																																	O/X

Lateral ethmoid — The lateral ethmoid bone begins to form at the anterior rim of the orbit early in the larval period. Late in the larval period (13.2 mm) the preorbital spine begins to form as a dorsal projection from the bone. Inconspicuous at first, it enlarges to become a prominent spine in juveniles and adults.

Nasal — The nasal spine begins to form at about 12.8 mm as a dorsal projection of the nasal bone. It becomes pronounced with further development and is a prominent spine in juveniles and adults.

Posttemporal — The posttemporal bone forms two spines. In the smallest stained larva a strong spine projects outward from the ventral margin of the bone. It remains conspicuous throughout the larval period but as the lower region of the bone begins to curve inward in pelagic juveniles the spine recedes, becomes barely discernible in early benthic juveniles, and then disappears. A second spine begins to form above the lower spine on the posterior edge of the bone at 10.0 mm. In contrast to the lower posttemporal spine, the upper spine becomes progressively larger with development. It projects dorsoposteriad from the bone and is retained in juveniles and adults.

Supracleithrum — A backward-projecting spine appears on the posterior edge of the supracleithrum at 8.2 mm. It enlarges progressively with development to equal the upper posttemporal spine in size and is retained in adults.

Cleithrum — A small spine appears on the upper posterior margin of the cleithrum at 14.7 mm. It remains throughout the pelagic period, is retained in small benthic juveniles, and then lost.

Interopercular — Late in the larval period a supporting rod begins to develop at the upper margin of the interopercular, where the bone faces the subopercular. At 15.7 mm this rod projects backward as a spine which is retained throughout the remainder of the stained series. It is variously present or absent in benthic juveniles and adults.

Subopercular — In some pelagic juveniles a spine projects from the lower margin of the subopercular, where the bone faces the interopercular. In the largest stained specimen (32.2 mm) a second spine is present just above the one at the lower margin. Like the interopercular spine, these spines are variously present or obsolete in benthic juveniles and adults.

A notable feature of head-spine development in *Sebastes* is the gradual ontogenetic appearance of most of the major spines found in other scorpaenid genera. Of the 22 spines that Eschmeyer (1969) has listed for the Scorpaenidae, 19 occur in the larvae and pelagic juveniles of *Sebastes*. In genera of the subfamily Scorpaeninae, the spines that develop in larvae and pelagic juveniles are retained and typically become more prominent in adults. In *Sebastes* (subfamily Sebastinae) a number of spines gradually become reduced toward the end of the pelagic juvenile stage and are lost soon after the fish settle. Among the spines that degenerate are the infraorbitals (which are, however, retained in *S. aleutianus*, *S. macdonaldi*, and *S. phillipsi*), the anterior preoperculars, the lower posttemporals, and the pterotics. Apart from the ontogenetic appearance and loss of these spines, other spines of the complement known for *Sebastes* are lost or reduced in adults of some species (Phillips 1957). Generally spine reduction and loss is more pronounced in species that have a convex interorbital region and a streamlined head, and usually do not live directly on the bottom. This trend culminates in semipelagic species such as *S. goodei*, *S. jordani*, and *S. paucispinis*, which have little or no spination atop the head. Interestingly, spination appears to be adaptive at one life-history stage and nonadaptive at another; i.e. sebastine larvae and pelagic juveniles develop almost the complete ancestral complement of head spines, probably as an adaptation for flotation and defense. As adults, the evolutionary direction of sebastines is toward a pelagic existence that contrasts with the sedentary mode of existence of most scorpaenines and, for this, the reduction and loss of head spines is adaptive in adults and is reflected in the loss of spines during ontogeny. In concert with this, the connection between the preopercle and infraorbital 3 is reduced to allow the flexibility and streamlining that would appear to be adaptive for semipelagic life. In scorpaenines, infraorbital 3 is a broad bone that fuses with the preopercle, whereas in *Sebastes*, infraorbital 3 is T-shaped and sends a narrow projection to the preopercle but does not fuse with it.

FIN DEVELOPMENT

In comparison with other *Sebastes* species, the pectoral fins of *S. melanostomus* are of moderate length. They increase in relative length during development (Table 3). The pectoral fin base is relatively deep as in *S. levis*. The smallest stained specimen has 17 pectoral rays, which falls within the adult complement of 17–20 (Table 6). For the remainder of the series the modal count is 19.

The pelvic fin is also of moderate length in comparison with other species and further enlarges during development (Table 3). The adult complement of 1 spinous and 5 soft pelvic rays is evident in the smallest stained specimen. In this specimen, 3 of the anterior spinous dorsal rays and 7 of the soft rays are forming. The full complement of 13–14 spinous rays is achieved in all larvae longer than 8.2 mm. Although the 13th spinous ray cannot be differentiated anatomically from the 1st soft-ray until the middle of the larval period, it is distinguished by its relative height. The most posterior

TABLE 6. Meristics from cleared and stained larvae of *S. melanostomus*.

Length (mm)	Procurrent caudal fin rays		Pectoral fin rays		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Vertebrae
	Superior	Inferior	Left	Right	Upper limb	Lower limb			
6.2 NL	2	2	17	17	2	15	0,5	III,7	23[a]
6.8	2	—	19	19	3	15	III,7	XIII,12	26
7.2	2	3	19	19	2	15	II,7	XII,11	24[a]
7.5 SL	3	3	19	19	3	16	III,7	XIII,12	26
7.7	3	4	20	20	3	15	III,7	XIII,11	26
8.2	4	5	17	17	4	17	III,7	XIII,13	26
8.8	5	6	18	18	6	16	III,7	XIII,13	26
9.0	5	6	19	19	6	17	III,7	XIII,13	26
9.4	5	6	18	19	5	17	III,7	XIII,13	26
10.0	7	8	19	19	7	20	III,7	XIII,13	26
10.6	7	7	19	19	7	18	III,7	XIII,14	26
11.8	8	8	19	19	8	20	III,7	XIII,14	26
12.0	8	9	20	20	8	19	III,7	XIII,13	26
12.8	8	8	19	19	8	21	III,7	XIII,13	26
13.2	9	9	19	19	8	20	III,7	XIII,13	26
13.5	9	9	19	19	8	21	III,7	XIII,13	26
13.8	9	9	19	19	8	19	III,7	XIII,14	26
14.2	9	9	20	20	8	21	III,6	XIV,14	26
14.7	9	10	19	19	8	20	III,7	XIII,13	26
15.7	9	10	19	19	8	21	III,7	XIII,13	26
16.0	9	9	19	19	8	21	III,7	XIII,14	26
16.9	9	9	19	19	7	20	III,7	XIII,14	26
17.7	10	10	19	19	8	21	III,7	XIII,13	26
18.4	10	11	19	19	8	21	III,7	XIII,13	26
18.9	9	10	19	19	8	21	III,6	XIII,13	26
19.5	9	10	19	18	9	22	III,7	XIII,14	26
20.3	9	10	19	19	8	21	III,7	XIII,14	26
21.1	10	10	19	19	8	21	III,7	XIII,14	26
22.4	9	9	19	19	9	22	III,7	XIII,13	26
26.9	—	—	19	19	9	22	III,7	XIII,13	26
32.2	—	—	20	19	8	21	III,7	XIII,13	26

[a] Incomplete vertebral count.

rays are the last to appear, and the ultimate ray is distinguishable by its bifid condition.

The smallest stained specimen has no spinous anal rays, but all specimens 7.5 mm and longer have the full complement of 3. As in the dorsal fin the most posterior spinous ray can be identified by its relative height. The full complement of 6–7 soft rays is present in larvae 6.8 mm and larger. As in the dorsal fin, the ultimate soft ray is bifid. All but 2 of the 30 specimens had 7 soft rays.

Formation of the caudal fin had already begun in our smallest specimens which are undergoing notochord flexion. Flexion is complete at 7.5 mm. Although juveniles have 2 superior and 2 inferior hypurals the more primitive complement of 3 + 3 hypurals is evident during the larval stage. In juveniles, the superior hypurals consist of a broad inner and a small upper bone; the inferior hypurals comprise a broad inner bone and a narrow lower bone, the parhypural, which we have included in our count of hypurals. These broad inner bones each start from two centers of ossification. In the superior group, the three hypurals start to ossify independently. The uppermost, a small hypural, forms rather late, since it was first observed as a cartilage at 10.6 mm and was not ossified until about 12.8 mm. The other two hypurals are evident on the smallest stained specimen, 6.2 mm. They remain as distinct bones on 6.2- to 7.7-mm specimens and then fuse, initially at their distal margins and then gradually inward toward the ural centrum; fusion was complete by ~17 mm. The inferior group also forms from three centers. On the 6.8-mm specimen, all three bones are separate and ossifying. The two inner bones are fused at their distal margins on a 7.2-mm specimen, and mostly fused along their lengths by ~8.2 mm; however, complete fusion can be delayed until ~17 mm. All hypurals are autogenous (separate from the ural centrum). In that it retains a hemal arch and has a pair of long, thin "parhypuropophyses," the lower hypural of the inferior group could be characterized as a typical "parhypural."

The 8+7 principal caudal rays, countable on the smallest specimen, are supported exclusively by the hypural bones; the superior hypurals support the 8 rays

TABLE 7. Change in the mean number and range of ventral midline melanophores in larvae of *S. melanostomus* from midwater trawl collections.

Size range (mm)	No. specimens	$\bar{x} \pm$ SD	Range
6.0–6.9	12	7.3±1.30	4–9
7.0–7.9	26	5.2±2.53	1–10
8.0–8.9	16	3.8±2.81	0–9
9.0–9.9	9	2.3±1.87	0–5
10.0–10.9	10	1.8±1.99	0–5
11.0–11.9	4	2.8±2.63	0–5
12.0–12.9	13	0.5±0.97	0–3
13.0–13.9	15	0.1±0.26	0–1

of the upper lobe and the inferior hypurals support the 7 rays of the lower lobe.

The procurrent caudal rays form gradually. Two dorsal and 2 ventral procurrent rays were detectable on the 6.2-mm specimen; the lower value for the full complement of procurrent rays, 9 dorsal and 9 ventral, was developed on a 13.2-mm specimen, and the more usual complement of 9 dorsal and 10 ventral rays on a 14.7-mm specimen. The range in larger specimens is 9 or 10 dorsal and 9–11 ventral. The ventral procurrent caudal rays are supported by the spatulate elongated hemal spines of the two vertebrae immediately anterior to the ural; the dorsal procurrent caudal rays are supported by the three epural bones and the spatulate, elongated neural spine of the second vertebra anterior to the ural. The reduced neural spine of the vertebra adjacent to the ural forms at 10.6 mm but is too short to enter into support of the procurrent rays. Note that both hemal spines that support ventral procurrent caudal rays develop autogenously, separate from their centra, but appear to be secondarily ossified to their centra in later life-history stages.

The ural centrum, a long moderately tapered bone with a truncate termination, is beginning to ossify on the 6.2-mm specimen. On this specimen, all vertebral centra except the three immediately anterior to the ural centrum are ossifying; by 7.5 mm all 26 vertebral centra are ossifying. The three epurals are first seen as cartilage on a 9.4-mm specimen and are ossified on a 13.2-mm specimen. The single pair of uroneurals appears on a 10.6-mm specimen and is well developed by 13.2 mm.

PIGMENTATION

The initial pigment pattern of *S. melanostomus* larvae is known from specimens reared in the aquarium (Moser et al. 1977). The dorsal and lateral surfaces of the gut are covered with melanophores. A ventral midline row on the tail contains fewer melanophores than in any other species presently known (mean of 8, with a range of 4–11, for 27 specimens counted). The pectoral fin is partially covered with a patch of fine melanophores. Most specimens examined had one or two spots on the nape, as many as 8 melanophores on the dorsal aspect of the head, and a strong patch at the mandibular symphysis, often extending onto the gular region. About half of the reared specimens had a linear patch of melanophores at the posterior aspect of the jaw, a unique placement for the species of *Sebastes*, insofar as presently known.

With further development, the number of melanophores in the ventral midline is reduced (Table 7) and they are lacking in larvae longer than 14.0 mm. The pigment over the gut is augmented and forms a solid sheet over the gut. Pigment is added to the brain and forms a solid covering in larvae longer than 11.0 mm. The blotch at the symphysis of the lower jaw enlarges to cover the oral valve and remains prominent throughout the larval period. It becomes diffuse and gradually weaker in pelagic juveniles and is absent occasionally in specimens longer than 18.0 mm. The pigment streak originally posterior to the jaw becomes more pronounced and becomes located above the anterior half of the maxillary throughout the larval and pelagic juvenile stages. A distinctive patch of melanophores begins to form on the upper region of the opercle in 6-mm larvae. The patch enlarges throughout the larval period. In pelagic juveniles it covers the entire opercle and becomes confluent with the dorsal head pigment. Pigment develops on the cheek at the posteroventral corner of the orbit in larvae as short as 10.8 mm. It is variously present or absent in larvae as long as 13.0 mm and present, usually as a triangular patch, in specimens up to 19.0 mm. In larger pelagic juveniles the patch usually extends anteriad beneath the eye. Pigment patches in the nasal region are present in about half the larvae longer than 13.0 mm. In pelagic juveniles the patches enlarge and become diffuse over the entire nasal region.

The most striking pigmentation is the pattern of melanistic bars that develops on the body. The anterior bar begins to form in larvae as short as 11.3 mm. Either a patch of melanophores that extends upward from the gut region or a patch that extends downward from the base of the dorsal fin, or both, are present. Although the smallest larvae in which these patches become confluent to form a complete band measures 12.3 mm, larvae as long as 14.7 mm may not have a complete band. The band has a consistent width, extending ventrad in a zone between the 3rd or 4th to the 7th or 8th spinous dorsal. A bar begins to form beneath the soft-dorsal fin in larvae as short as 14.4 mm. It is present in about half of the larvae between 14.4 and 16.0 mm as a patch of melanophores or saddle extending ventrad from the fin base. It was observed in all but 4 of 21 pelagic juveniles between 16.0 and 18.2 mm long and in all specimens longer than this. There is a gradual ventrad progression of the saddle, and in late pelagic juveniles a complete band is formed with pigment developing dorsad from the anal fin base. A third band begins to form on the caudal peduncle in pelagic juveniles as short as 20.7 mm. Initially it is a lateral blotch but enlarges to form a complete band in specimens longer than 32.2 mm.

The development of background pigment on the unbanded regions of the trunk is a gradual process that begins in larvae as short as 13.5 mm in which one to several melanophores appear forward of the anterior band. These melanophores become more extensive in later larvae, and the entire area anterior to the band begins filling in with pigment in pelagic juveniles to become solidly covered in most specimens longer than 19.0 mm. The gradual filling in of the unpigmented areas between the posterior bands begins at ~32.5 mm long and progresses so that the largest pelagic juvenile is completely pigmented with the bands merely accentuated.

The fins are also characteristically pigmented. In newborn larvae the pectoral fin blades are evenly covered with fine melanophores. As the fin rays develop, the melanophores become distributed on the interradial membranes, with heavier pigmentation on the distal margins of the blades. The medial surfaces of the fin bases are heavily pigmented. At ~7.5 mm an unpigmented zone begins to form between the distal margin and the proximal half of the fin blade. At ~9.0 mm the pigment at the distal margin begins to diminish while pigment remains in an arc-shaped basal zone that extends onto the dorsal margin of the fin. At the beginning of the pelagic juvenile stage the pigment along the dorsal margin of the fin begins to recede, leaving a basal bar that becomes accentuated in late-stage pelagic juveniles. In early larvae the membranes between the pelvic rays become covered with melanophores, and the distal margins of the fins are accentuated. At ~9.0 mm the pigment begins to recede from the margins and with further development becomes restricted to the proximal region of the fins.

Characteristic blotches develop on the dorsal and anal fins of pelagic juveniles. At the beginning of the pelagic juvenile stage a large blotch develops as a dorsad extension of the anterior pigment bar and at its maximum development in late-stage pelagic juveniles occupies the basal half of the fin in a zone extending from the 3rd to the 6th spinous ray. Concomitantly, a small blotch develops anteriorly on the membrane between the 1st and 3rd spinous rays. At ~26.0 mm a large blotch develops as a dorsal extension of the posterior pigment bar and another blotch forms between the 9th and 12th spinous dorsal rays. At ~30.0 mm a blotch forms on the anal fin and at maximal development extends from the 2nd spinous ray to the 7th soft ray.

DISTRIBUTION

Confusion surrounds our knowledge of the latitudinal range of *S. melanostomus*. Miller and Lea (1972) listed the southern limit as Cedros Island, Baja California (28°15′N). Our records extend this southward to off Punta Abreojos (26°06′N, 114°05′W). On the basis of biochemical identification Tsuyuki and Westrheim (1970) suggested that the northern limit lies to the south of British Columbia. Barsukov (1968) reported this species from the Bering Sea and synonymized it with the Japanese species *S. iracundus*. If he is correct, *S. melanostomus* has the greatest latitudinal range of any species of *Sebastes*. Tsuyuki and Westrheim (1970) pointed out the taxonomic complexities of the *S. melanostomus* species group and their estimate of the northern limit of this species may well be correct.

Little is known about the bathymetric distribution of *S. melanostomus*. Depth range for 10 benthic collections of juveniles and adults made off southern and Baja California was 183–448 m with a mean weighted to catch rate of 302 m (SIO Fish Collection). Miller and Lea (1972) listed the maximum known depth of *S. melanostomus* as 549 m, making this one of the deepest living of all *Sebastes*. For this reason, blackgill rockfish are rarely taken by commercial and recreational fishermen off southern California. Their comparative abundance in midwater trawl samples in this area (Table 1) suggests that the small catches of adults may not reflect true abundance and that blackgill rockfish may represent a potential deep-water fishery.

The frequent and widespread occurrence of larvae and pelagic juveniles in midwater trawl samples taken over deep coastal waters (Fig. 1) and their need to reach more shoreward shallow areas for settling suggests a distinct life-history strategy for *S. melanostomus* and for the other rockfish species taken with it.

The peak month for birth of *S. melanostomus* larvae off southern California is February (J. LaGrange personal communication). Like other species of *Sebastes*, larvae of *S. melanostomus* inhabit the upper mixed layer and are seldom taken below 100 m (Ahlstrom, 1961). After completing larval development at ~16 mm long they transform into pelagic juveniles and live in the midwaters over coastal basins during summer. Large *S. melanostomus* larvae appear in midwater trawls from April to August (Fig. 8). Pelagic juveniles begin to appear in June and are found in increasingly larger sizes through October. Examination of daily growth rings on the otoliths of specimens taken from albacore stomachs revealed an age of 47 d for a 15.0-mm larva and 101 d for a 30.4-mm pelagic juvenile, the largest one available (Fig. 9). Pelagic juveniles are therefore ~3½ mo old when they approach the size for settling. The size threshold for settling to the bottom is ~36.0 mm, judging from a newly transformed specimen of that size taken in an otter trawl off Scripps Institution of Oceanography (La Jolla, Calif.) at 265–356 mm. Pelagic juveniles of this size appear in midwater trawls in September and October and either migrate or are transported shoreward to water of appropriate depth for settling. Two discrete depth tows, one at 200 m in August and another at 250 m in October, contained pelagic juveniles of 30.1 and 32.5 mm, respectively, suggesting that horizontal migration or transport of pelagic juveniles occurs in this depth range. This strategy appears to be shared with *S. aurora* and a number of

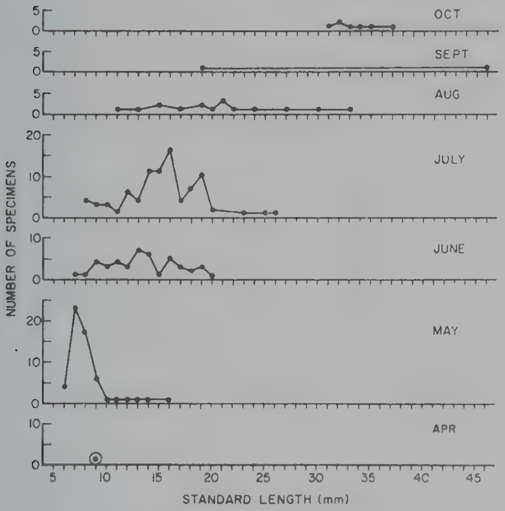


FIG. 8. Composite monthly size frequencies for larvae and pelagic juveniles of *S. melanostomus* from midwater trawls.

species of the subgenus *Sebastomus*. Interestingly, all of these species have strong dark bands alternating with almost transparent regions on their bodies, possibly a protective pattern that serves to break up their body outline during their pelagic life. A similar strategy involving a midwater pelagic juvenile stage is found in *Sebastolobus altivelis*; however, adults of that species inhabit the deep coastal basins and juveniles can reach the adult habitat by descending vertically (Moser 1974).

A different strategy is employed by the splitnose rockfish, *Sebastes diploproa* (Mitchell and Hunter 1970; Boehlert 1977). Larvae are released from February to July and appear in surface waters upon reaching a length of ~10 mm. They are recruited to drifting masses of kelp and flotsam where they grow to a maximum of 50 mm long. These juveniles develop a solid background pigmentation with faint bars, and the fins have contrasting dark and clear areas that would appear to disguise them in the kelp and midwater habitat. Since the smallest benthic specimens are ~30 mm long, emigration from surface waters must occur in a length range of 30–50 mm. Catches from discrete midwater hauls indicate that emigrating pelagic juveniles descend to a depth of 200–250 m and migrate horizontally until they reach bottom, at which time they are ~1 yr old.

The bocaccio, *S. paucispinis*, exhibits a third strategy (Moser 1967). Planktonic larvae attain a size of ~30 mm and then migrate shoreward to their early juvenile habitat in kelp and eelgrass beds. Juveniles from these habitats have a striking pattern of irregular bars and pigment saddles that provide a mottled appearance. At the end of their 1st yr they begin to move into deeper water, and a pattern of small spots has replaced the mottling.

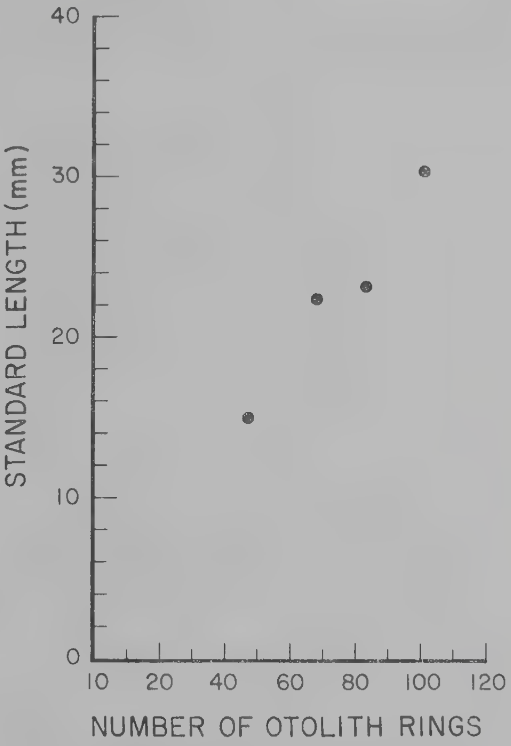


FIG. 9. Age–length relationship of *S. melanostomus* based on counts of daily growth rings of sagittae.

The life-history strategies described here are probably only a fraction of those utilized by wide-ranging planktonic larvae of rockfishes to reach appropriate habitat for settling. At present the larvae of only about a half dozen species can be identified from plankton samples and, with present techniques, the larvae of a substantial number of species will not be differentiable. Estimation of spawning biomass from ichthyoplankton surveys will therefore be limited to a portion of the rockfish fauna. Likewise, the commercial and recreational fisheries sample a limited number of species over a portion of their habitat. An alternative is to sample juvenile stages. Because of the diversity of strategies and habitats, each species may be vulnerable to collection at some time during the juvenile period, either by trawl, trap, or predator. Additionally, sampling of juvenile stages provides the potential for predicting year-class strength. *Sebastes melanostomus* provides a clear example of a species with a special pelagic juvenile stage that is vulnerable to sampling by midwater trawl. Research on the life histories of other rockfish species may provide similar opportunities for resource assessment.

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FISH BULLETIN 167

CLIMATIC VARIATION AND EXPLOITATION IN THE PACIFIC MACKEREL FISHERY

by

RICHARD H. PARRISH
National Marine Fisheries Service
Monterey, California

and

ALEC D. MacCALL
California Department of Fish and Game
La Jolla, California

1978

ABSTRACT

This bulletin provides an in-depth analysis of the California Current Pacific mackerel (*Scomber japonicus*) fishery. It includes descriptions of the fishery and the species population biology, a cohort analysis, density and environmental-dependent spawner-recruit models, and yield simulations. The cohort analysis (1928–1968), using an instantaneous natural mortality rate of M = 0.5, shows a fluctuating stock size with a maximum total biomass of 965 million pounds (438,000 MT) in 1933 and a minimum of 3.3 million pounds (1500 MT) in 1968. The number of recruits-per-spawner shows large fluctuations with considerable coherence between adjacent years. There was no marked downward trend in recruits-per-spawner over the 1928–1968 period. Density-dependent spawner-recruit models accounted for a maximum of 24 percent of the observed variation in recruitment. Multiple regression models, including both population and environmental variables, were fitted to the data available for two time periods; 1931–68 and 1946–68. The 1931–68 model accounted for 59 percent of the variation in recruitment; increased recruitment was associated with increased sea surface temperature, reduced sea level and reduced atmospheric pressure during the spawning season. The 1946–68 model accounted for 76 percent of the variation in recruitment; increased recruitment was associated with increased coastal upwelling and decreased offshore convergence during the spawning season. Maximum yield-per-recruit occurs with an age at recruitment of 1 or less, and with instantaneous fishing mortalities (F) in excess of 1.0. A dynamic pool model incorporating a Ricker spawner-recruit model predicts that extinction of the stock will occur with the above fishing strategy. Maximum sustained yield (MSY) with the steady state dynamic pool model is above 94 million pounds (41,000 MT). This MSY occurs with an age-at-recruitment of 4 and with an exploitation rate of 0.25. Simulations incorporating the density and environmental-dependent spawner-recruit functions predict that the above MSY cannot be attained when there is serial coherence in the annual recruitment fluctuations. Mean longterm annual yield with the above fishing strategy, under the environmental conditions occurring between 1931–1968, would have been only 56 million pounds (25,000 MT). With an age-at-recruitment of 1, maximum steady state yield (69 million pounds, 31,000 MT) occurs at an exploitation rate of 0.2. Maximum longterm yield with this fishing strategy, under the 1931–68 environmental conditions, would have been 45 million pounds (20,000 MT).

TABLE OF CONTENTS

Page
ABSTRACT 2
LIST OF TABLES 4
LIST OF ILLUSTRATIONS 5
ACKNOWLEDGEMENTS 7
INTRODUCTION 9

THE FISHERY

Stock definition 11
History of the Fishery 13
Management of the Fishery 15
Catches 17
Age composition 18

POPULATION BIOLOGY

Growth 25
Reproduction 26
Schooling 28
Natural mortality rate 30

COHORT ANALYSIS

Estimation of fishing mortality rates 37
Population estimates 39
Recruitment and spawning success 42

RECRUITMENT MODELS

Methods 49
Density-dependent recruitment functions 54
Associations between recruitment and environmental factors 57
Environmental-dependent recruitment functions 64
Factors affecting recruitment 65

COMPUTER SIMULATIONS

Simulation models 71
Yield per recruit model 73
Equilibrium yield simulations with density-dependent recruitment 73
Yield with environmental-dependent recruitment functions 78
Annual yield under four management options 80

DISCUSSION

Evaluation of recruitment models and simulations 85
Alternative management plans 89
REFERENCES 92

APPENDICES

Appendix I 97
Appendix II 101
Appendix III 108

LIST OF TABLES

Table — Page

1 Tag return rates by geographical area as an index of relative availability of fish to the fishery (based on Fry and Roedel, 1949). 12

2 Season catches of Pacific mackerel from 1926–27 to 1969–70 (weights in 1000 lb) 17

3 Pacific mackerel ratios of total catch to aged catch (weights in thousands of pounds). 19

4 Validation of unpublished otolith readings. 20

5 Comparison of estimated age composition of early Pacific mackerel catches by NORMSEP and by otolith readings. 20

6 Catches by age and season (1000 Fish). 22

7 Length and weight by age of Pacific mackerel (From Knaggs and Parrish 1973). 25

8 Catch curve estimates of total mortality rates from length frequency and von Bertalanffy growth curve ($L_\infty = 404.6$ mm, $K = 0.221$) 32

9 Abundance index, effort index and total mortality rate estimates for Pacific mackerel. 33

10 Estimates of natural mortality rate for Pacific mackerel. 35

11 Comparison of the effect of different assumed values of F for the 1969–70 season on the time series of fishing mortality rate estimates for fully recruited fish. 38

12 Approximate rates of convergence for cohort analysis, backward solution, $M = 0.5$, as determined by simulated catches. 39

13 Fishing mortality rates by season. 40

14 Beginning of season biomass estimates. 44

15 Comparison of spawning success for two periods of the Pacific mackerel fishery. 46

16 Regression variables for spawner-recruit functions. 50

17 Density-dependent spawner-recruit functions. 55

18 Correlation coefficients of linear combinations of monthly values of environmental variables in 1n (R) 63

19 Environmental-dependent spawner-recruit functions. 66

20 Alternative management options. 90

LIST OF ILLUSTRATIONS

Figure Page

1 Pacific mackerel landings in California (1926–1970). 14

2 The relationship between total biomass and the proportion of age 1 spawners. 27

3 Distribution and relative abundance of Pacific mackerel larvae in 1955 (fig. 20 of Kramer, 1960). 29

4 Pacific mackerel comparison of length frequency for 1929–30 and 1930–31. 31

5 Pacific mackerel Von Bertalanffy growth curve parameter estimation. Data for D.H. Fry otolith readings 1933–1934.................... 32

6 Estimation of M by the relationship of Z to F.................... 34

7 Total biomass of the California Current stock of Pacific mackerel. 42

8 Spawner-recruit relationship.................... 43

9 Time series of the natural log of the observed recruit biomass per spawning biomass.................... 46

10 Density-dependent spawner-recruit models; A. Ricker, B. Beverton and Holt, C. Cushing.................... 49

11 Marsden Square quadrants 120 (2) and 84 (3), and upwelling index locations. 52

12 Natural logarithms of recruit biomass per spawning biomass plotted against spawning biomass (including fitted regression). 56

13 Ricker and Cushing spawner recruit models fitted to Pacific mackerel population data (Values in millions of lbs). 57

14 Ricker and Cushing spawner resultant-spawner models (values in millions of lbs).................... 58

15 Correlations of ln (R) with monthly environmental factors; A. SST in Marsden Square 120 (2), B. SST in Marsden Square 84 (3), C. SST at Scripps Pier, D. Sea Level differences from Saur (1973), E. Sea level barometric pressure at San Diego, F. Sea level at La Jolla. 59

16 Correlations in ln (R) with monthly environmental factors; A. Wind speed in Marsden Square 120 (2), B. Wind speed in Marsden Square 84 (3), C. Cloud cover in Marsden Square 120 (2), D. Cloud Cover in Marsden Square 84 (3). 60

17 Correlations of ln (R) with monthly environmental factors; A. Meridional Ekman transport at 30°N, B. Meridional total transport at 30°N, C. Bakun's (1973) upwelling indices at 30°N, D. Offshore divergence indices at 30°N (Bakun pers. comm.). 61

18 Wind stress curl patterns off of Southern California and Baja California (Bakun and Nelson In Press). 62

19 Observed and predicted recruitment of Pacific mackerel; A. Ricker sea level model, B. Ricker transport model.................... 66

Figure Page

20 ISOE simulations with $M = 0.5$; A. Yield per unit weight of age 1 recruits, B. Resultant spawning biomass per unit weight of age 1 recruits. 74

21 Pacific mackerel biomass curve with no fishery and $M = 0.5$. 75

22 QUOTAE equilibrium yield isopleths with density-dependent spawner-recruit functions (Yield in millions of lbs) 76

23 QUOTAE equilibrium yield isopleths, at four different sets of quota levels with the Ricker nonlinear model (Yield in millions of lbs, quota based on spawning biomass). 77

24 QUOTAE mean yield isopleths (1931–1968), at different sets of quota levels, with the Ricker sea level model (Yield in millions of lbs, quota based on spawning biomass). 79

25 QUOTAE mean yield isopleths (1946–1968), at four different sets of quota levels, with the Ricker transport model (Yield in millions of lbs, quota based on spawning biomass). 80

26 QUOTAE simulations (1946–1968); A. Recruitment at age 1 no minimum quota level and a quota proportion of 0.7 (w in figs 21A and 22A) B. Present California Regulations recruitment at age 1 and an upper quota proportion of 0.3 (x in figs 21B and 22B) ... 81

27 QUOTAE simulations (1946–1968); A. Recruitment at age 2 and an upper quota proportion of 0.4 (y in figs 21B and 22B) B. Recruitment at age 4 and an upper quota proportion of 0.5 (z in figs 21B and 22B) 82

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INTRODUCTION

The objectives of this work are to assess the role of environmental variation in the decline of the California stock of Pacific mackerel (*Scomber japonicus*) and to evaluate the merits of using environmental data in management policies for this species. The study is principally focused upon three areas. The first is a cohort analysis of the stock. The second is the development of density and environmental-dependent regression models that describe recruitment in the above stock. The third is the use of these regression models in dynamic pool computer simulations to describe the types of management policies that are likely both to decrease the possibility of another recruitment failure and to maximize the long-term yield from the stock.

The Pacific mackerel fishery has been monitored extensively and studied since its beginning in the 1920's. Unfortunately the proper tools and background information for analysis of the fishery were not available until the mid 1960's, by which time the fishery was undergoing its final collapse. Now that the population biology and fishery dynamics are sufficiently understood, there is a real possibility of eventually rehabilitating the fishery and sustaining a reasonable level of exploitation.

This study is based on a cohort analysis of catch data similar to that developed by Murphy (1966) for analysis of the sardine fishery. Necessary steps leading to use of this technique and interpretation of the results include delimitation of the stock, compilation of catches of each year-class, and estimation of important population parameters. These parameters are rates of growth, natural mortality, maturity, and age of recruitment. Cohort analysis produces estimates of fishing mortality rates and population sizes which then can be applied to comprehensive models of the population and its fishery.

Many of these investigations have been undertaken by previous workers, and due credit must be given. Unfortunately little of the previous work reached publication, although Blunt and Parrish (1969) and Parrish (1974) incorporated some of those previous findings. Patrick Tomlinson did extensive work using cohort analysis and Norman Abramson later continued the research. The present study uses few data and parameter estimates from those studies; however, many assumptions, methods, and techniques which were developed and tested by Tomlinson and Abramson are used, directly or indirectly.

Over the last decade increased attention has been focused on the stock and recruitment problem of commercially important fishes. If any consensus exists in the large amount of published data it is that the major factor affecting recruitment is larval survival. The mechanisms controlling larval survival, of course, may vary from stock to stock. Some workers suggest that a critical stage occurs at the time of first feeding (Hjort 1926; Lasker 1965). Other workers feel that the critical period extends for up to 45 days (Jones and Hall 1973).

Most of the recent research into the recruitment problem has been divided into two phases: laboratory and field experiments on larval fish biology, and population dynamics models. The development of models has been dominated by conceptual work; a statistical approach to the problem has been limited by the lack of long-term data on both fish populations and environmental conditions. Long-term data are becoming available for statistical analyses and workers are beginning to develop multiple regression models utilizing environmental and density-dependent variables (Nelson et al. 1976). One of the best long-term data bases available for statistical analyses of the associations between recruitment of pelagic fishes and environmental conditions is that of the California Current region. This extensive data base is largely the result of the multidisciplinary approach of the California Cooperative Oceanic Fisheries Investigations (CalCOFI).

We have used the CalCOFI data base to determine associations between the recruitment of Pacific mackerel and environmental variables. Recruitment models including density parameters and both density and environmental parameters were then developed with regression procedures. These recruitment models were incorporated in computer simulation models to assess the differences in their predicted yields. The results of the simulations were analyzed to examine the relative merits of managing the fishery on two different policies; that is, a policy based on a yield per recruit model and a policy based on dynamic pool simulations incorporating both density-dependent and environmental-dependent factors.

Previous work on recruitment in Pacific mackerel has been limited to density-dependent recruitment models. Ricker spawner-recruit models were described by Blunt and Parrish (1969) and Parrish (1974). The present work is the first to incorporate long-term environmental data in recruitment models of a California Current stock and to use observed environmental data as inputs to simulations using such models.

THE FISHERY

STOCK DEFINITION

Scomber japonicus occurs on both sides of the North Pacific and on its eastern edge ranges from the Gulf of Alaska to the Gulf of California. The bulk of the Northeastern Pacific population resides off southern California and Baja California. As the fishery for Pacific mackerel has been pursued mainly in southern California rather than over the entire range of the species, the problem of geographically defining the stock being exploited is difficult. Rather than being a set fraction or geographical subset of the entire population, the stock is defined vaguely by rates of migration and diffusion of fish along the coast, rates which vary both seasonally and annually.

A tagging study (Fry and Roedel, 1949) showed a progressive decrease in likelihood of returns as the area of release became more distant from the fisheries which recovered the tags. Assuming that the rate of local tag returns from fish released in the same area as the main fishery represents full availability, relative rates of returns from fish released in more distant areas provide measures of relative availability (RA) of fish from those areas (Table 1). Thus we find that most of the fish from central California are available to the southern California fishery (RA = 0.88), while the converse is not true; fish from southern California are much less available to the central California fishery (RA = 0.23). Availability of fish from Mexican water declines steadily with distance, showing no abrupt edge to the exploitable population. Relative changes in availability with distance for these southern fish show close agreement between central and southern California fisheries. Unfortunately the years in which this tagging study was done (1939–41) correspond to a period of warm water conditions in the northeastern Pacific. Such warm conditions are conducive to strong northward migrations of many southern species of fish (Radovich 1961), and the Pacific mackerel, a known migrant, probably was affected. Thus these return rates may overestimate availability of southern fish to the California fisheries in years of normal oceanic conditions.

Another approach to stock definition was attempted by Roedel (1952), who studied both vertebral meristics and proportional measurements of head and fork lengths. Based on vertebral characters, populations from the Gulf of California and from the Cape San Lucas area were distinguishable from more northerly fish. The northern samples showed significant statistical differences for the Sebastian Vizcaino Bay, Soledad Bay (Ense-

TABLE 1. Tag Return Rates by Geographical Area as an Index of Relative Availability of Fish to the Fishery (Based on Fry and Roedel, 1949).

Area of release	*Number released*	*Southern Calif. fishery*		*Central Calif. fishery*	
		0/00 returned	*Relative avail.*	*0/00 returned*	*Relative avail.*
Central Calif. (Monterey Bay)	6,986	24.6	0.88	11.0	1.00
Southern Calif.	32,696	28.1	1.00	2.5	0.23
Northern Baja Calif. (San Quintin Bay)	3,937	20.3	0.72	0	
Central Baja Calif. (Sebastian Vizcaino Bay)	8,117	13.3	0.47	0.9	0.08
Southern Baja Calif. (Thurloe and San Roque Bays)	7,869	6.9	0.25	.04	0.04

nada) and Southern California areas when samples for individual regions were combined and compared by analysis of covariance. Roedel concluded that there was probably little mixing between these areas. As Roedel (1952) admits, these conclusions are not compatible with information from tagging studies.

Two reasons for this inconsistency can be postulated. First, as Roedel (1952) showed, even schools from the southern California area showed significant statistical differences, suggesting that populations tend to be much more heterogeneous than are individual schools. Such a condition is consistent with a north-south migration wherein schools retain their identity. Also, the presence of significant statistical difference between schools within geographic regions makes it difficult to interpret differences between geographic regions from combined samples. The second sources of possible inconsistency relates to the season in which sampling was done. If migration of Pacific mackerel follows a pattern of northward movement in early summer and southward movement in late fall, the samples on which measurements were made tend to be biased against migratory members of the population. Most of the southern California samples were taken in the winter and spring when migrants would be at the southern end of their range, and Sebastian Vizcaino Bay samples were taken in the fall when migrants would be north. Roedel's samples suggest a clinal variation in relative head length, and apparent discontinuities possibly would be smoothed if sampling were distributed over the entire year.

Combined evidence, from both meristic and tagging studies indicates that the spawning stock fished by the California fleet extends from British Columbia to Point Abreojos. Mixing of fish throughout this range is incomplete, so that fish at the ends of the range tend to be unavailable to the localized California fisheries. Since the fishery in Sebastian Vizcaino Bay was viable after the decline of the stock in California waters, there is also *de facto* evidence that fish at the southern end of the stock are effectively isolated from the California fishery.

HISTORY OF THE FISHERY

The development and subsequent decline of the Pacific mackerel fishery has been well documented in the literature. Croker (1933) discussed the early history of the fishery including fishing areas and the development of mackerel canning in California. Descriptions of the fishery during and after its peak include those by Croker (1933, 1938), Roedel (1952), Fitch (1952), and Roedel and Joseph (1954). The fishing gear used in the fishery was principally round-haul gear, primarily purse seine, and scoop gear (Fry 1931; Croker 1933; and Scofield 1947, 1951). More recent reviews of the fishery include Blunt and Parrish (1969), Kramer (1969), and MacCall (1973). Recent status reports showing current condition of the stock were prepared by Frey and Knaggs (1973) Knaggs (1974), Knaggs and Sunada (1975) and Klingbeil (1976).

Prior to the 1928–29 fishing season Pacific mackerel was primarily a fresh fish item and was fished both in Monterey and in southern California. Market demand was too small to generate interest among the round-haul net fishermen. After several attempts, a successful pack was made in the late 1920's and increasing cannery demand resulted in large catches by boats which had been fishing for sardines (Figure 1). The economic depression of the early 1930's caused a large drop in fishing effort, but a recovery of demand and prices made fisheries profitable once again and the fishery expanded from 1932–35, reaching a peak catch of 73,000 tons in 1935. Thereafter the fishery went through a long fluctuating decline, with periodic decreases in abundance followed by recoveries. In the 1953–54 season the fishery was nearly exhausted, but good recruitment in the 1950's rejuvenated the fishery until a series of poor recruitment years in the 1960's brought the fishery to a close. In the early 1970's a moratorium was placed on the fishery.

Two independent fleets fished for Pacific mackerel: the purse seine fleet, which was nearly identical with the sardine fleet, and the scoop fleet which was a mixture of specialized mackerel fishermen and off-season albacore fishermen. The purse seine fleet used no specialized techniques, but the scoop fleet had unusual fishing methods. These small boats began fishing in the early 1930's with lift poles and jigs (known as "striker gear"), but soon discovered that the fish could be chummed to such a concentrated frenzy that quantities could be scooped out of the water with a large dip net, hence the name. This fleet was a major component of the fishery, often accounting for over half the annual catch. The scoop fleet, severely affected by the shortage of fish in the early 1950's, fell from 348 full-time boats (6 or more days fished in the peak month) in 1949 to 10 full-time boats in 1952. As the fishing technique was highly specialized for this one species, the scoop fleet never fully recovered, and it finally disappeared in the mid 1960's. The purse seiners, which were able to switch to other species and were interested in Pacific mackerel as an alternative to the more lucrative sardine, survived the shortages of mackerel and sardines and continued fishing the species until a moratorium was imposed in 1970.

The fishing season followed a fairly set pattern until the mid 1950's. Fish

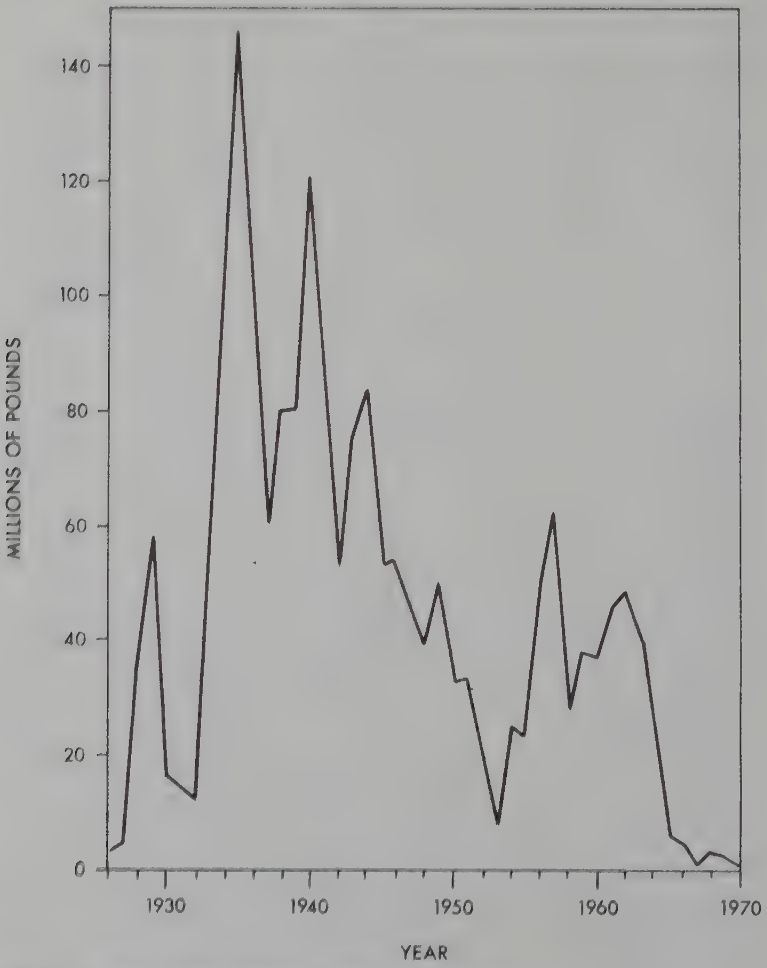

FIGURE 1. Pacific mackerel landings in California (1928–1970)

were relatively unavailable in southern California from January through May, and then increased in availability until late fall. Purse seiners accounted for most of the catch up to September when the sardine season began. A few scoop boats would fish all year, supplying fresh fish markets, which preferred scoop-caught fish to purse seined fish as they sustained less injury. The main scoop fishing season was in the fall, from August through December. In the declining years of the fishery catches became sporadic, losing any definitive seasonal pattern.

The sport landings of Pacific mackerel have been of relatively minor importance in the total marine sport landings. Young (1969) ranked them as the eleventh most important species in the southern California partyboat fishery. The mean catch from 1947–1967 was 127,921 fish. Only trace amounts of Pacific mackerel occur in the northern California partyboat catch.

Pinkas, Oliphant and Haugen (1968), ranked the most important sport fish caught in southern California marine waters from 1963–1966. They found Pacific mackerel to be the eighth most common species in the total marine sport fish catch; it comprised 3.2% of the fish caught. Since the commercial fishing moratorium was declared in 1970, the sport fishery has become the largest exploiter of the Pacific mackerel resource in California (MacCall, 1973).

MANAGEMENT OF THE FISHERY

Attempts to control or manage the Pacific mackerel fishery were unsuccessful until the stock had collapsed. A moratorium was then enacted by the California Legislature. During the period of 1936–1970 research personnel, principally from the California Department of Fish and Game and later the National Marine Fisheries Service and Scripps Institution of Oceanography, made several major attempts to control the fishery. Management proposals generally concerned both the Pacific mackerel and sardine. Blunt and Parrish (1969) have discussed the past management proposals for Pacific mackerel. An excellent review of the sardine-anchovy regulation controversy was given by Talbot (1973) and much of his account of the sardine is equally true for Pacific mackerel. Messersmith's (1969) treatment of the anchovy controversy provides considerable documentation of the problems of managing the pelagic fisheries of California.

The most recent attempt to regulate the Pacific mackerel fishery was associated with the anchovy-sardine controversy and began about 1967. The spawning biomass of Pacific mackerel had declined rapidly due to a long series of years with poor recruitment. Warnings of this decline (Parrish 1968; Blunt and Parrish 1969) and of the continuing critical situation with the sardine (Aasen 1967) accompanied the descriptions of underexploited species such as the anchovy (Messersmith et al. 1969, Ahlstrom et al. 1967), squid, (Longhurst 1969) and saury (Smith and Ahlstrom 1970). The scientific community was in the politically unenviable position of arguing for increased harvest of the anchovy at the same time it was recommending complete closure of the commercial fishery for sardine and Pacific mackerel.

In response to continuing requests to enact moratoriums on Pacific mackerel and to halt the bait fishery on sardine, the California Legislature requested the California Department of Fish and Game to arrange meetings with Mexican scientists to determine the exact status of the resource (MacCall 1973). In the fall of 1972 cooperative research was undertaken. However, the continued decline of Pacific mackerel off California and the increasing fishing mortality, which had by then become very heavy even on age 0 Pacific mackerel, encouraged the California Legislature to enact a unilateral moratorium on the commercial fishery for Pacific mackerel. This moratorium allowed an 18% tolerance for Pacific mackerel in mixed loads.

In 1972 the California Legislature enacted a bill that imposed a quota based on the spawing biomass of the Pacific mackerel. The regulation maintains a moratorium until the spawning biomass exceeds 20 million pounds. If the spawning biomass exceeds 20 million pounds (lower quota level) the annual quota consists of 20% of the excess over 20 million pounds. If the spawning biomass exceeds 40 million pounds (upper quota level) the quota consists of 20% of the amount between 20 million and 40 million pounds plus 30% of the excess over 40 million pounds.

The California Department of Fish and Game began monitoring the spawning biomass of the Pacific mackerel stock in 1973, as required by the above legislation. The subsequent trends are given in Frey and Knaggs (1973), Knaggs (1974), Knaggs and Sunada (1975), and Klingbeil (1976). The spawning biomass declined from 1973 to 1975 due to continued poor recruitment. The 1974 and 1976 year classes were relatively strong, and the spawning biomass has increased since 1975. A preliminary estimate of the spawning biomass for 1977 is 14,200 tons with an expected increase later in the year due to maturation of fish from the 1976 year class (Klingbeil, 1977). A tentative 1500 ton quota for the fall of 1977 has been recommended.

Fishery complications arose in 1977, and further legislation has complicated the management of the Pacific mackerel. The southern California purse seine fleet has expanded its jack mackerel (*Trachurus symmetricus*) fishery and the 1976 year class of Pacific mackerel was schooling extensively with jack mackerel. Although the previous legislation allowed an 18% tolerance of Pacific mackerel incidentally caught in harvests of other species, the purse seine fleet was consistently exceeding this tolerance limit. Compromise legislation was quickly passed, allowing a 40% incidental catch, with the fraction in excess of 18% applying toward filling the quota prior to the opening of the fishing season. A clause was included whereby pure loads of less than three tons could be landed anytime, and be applied toward filling the quota. This latter provision has allowed the reappearance of a scoop fishery which has begun to harvest Pacific mackerel. Fishing pressure is increasing alarmingly, considering that the spawning biomass is probably still smaller than at any time before 1965. On the other hand, the strong 1976 year class may be able to withstand this assault and maintain the trend toward recovery.

The emergency legislation referred to in the preceding paragraph was designed as an interim measure and it expired on January 1, 1978. Unless further legislation is passed, the 1972 regulations will automatically be in effect after January 1, 1978. For the purposes of this report the 1972 regulations will be referred to as the present regulations and the emergency 1977 regulations will be referred to as the interim regulations.

CATCHES

Pacific mackerel are landed by three separate fisheries: the California commercial fishery, the Mexican commercial fishery, and a diverse sport fishery which is based primarily in southern California. Documentation of catches of these fisheries is variable in format, and in some cases is lacking, making rough conversions and estimates necessary to compile total season catches (Table 2). A fishing season of May through the following April is used in published age compositions, and therefore will be used in estimation of total catch. California commercial landings have accounted for the majority of catch and fortunately are well documented. While some prob-

TABLE 2. Season Catches of Pacific Mackerel from 1926–27 to 1969–70 (Weights in 1000 lb)

Season	*Calif.*	*Mexico*	*Sport*	*Total*
1926–27	3594		50	3644
1927–28	6455		50	6505
1928–29	39405		50	39455
1929–30	56695		50	56745
1930–31	12806		100	12906
1931–32	15152		100	15252
1932–33	10850		100	10950
1933–34	72874		100	72970
1934–35	113464		200	113664
1935–36	146387		200	146587
1936–37	100745		200	100945
1937–38	70446		200	70646
1938–39	76065		200	76265
1939–40	99961		200	100161
1940–41	107555		200	107755
1941–42	71755		100	71855
1942–43	48220		100	48320
1943–44	77804		100	77904
1944–45	80786		100	80886
1945–46	52003		100	52103
1946–47	58896	1877 *	100	60833
1947–48	39628	2783 *	296	42707
1948–49	38203	1135 *	406	39744
1949–50	50062	2980 *	190	53232
1950–51	33890	4473 *	134	38497
1951–52	31905	2911 *	94	34910
1952–53	20218	2320 *	154	22692
1953–54	8829	2595 *	122	11546
1954–55	27210	12524 *	630	40364
1955–56	26897	21601 *	302	48800
1956–57	57184	23644 *	242	81070
1957–58	56238	4485 *	304	61027
1958–59	24777	989 *	274	26040
1959–60	41282	1092 *	178	42552
1960–61	39074	6573 *	158	45805
1961–62	44301	13149 *	228	57678
1962–63	45254	7124	234	52612
1963–64	34211	17561	294	52066
1964–65	24875	18999	202	44076
1965–66	7589	16788	304	24681
1966–67	4075	11662	410	16147
1967–68	1382	2091	216	3689
1968–69	3289	236	158	3683
1969–70	1783	443	240	2466

* Estimated

lems exist in estimating the poundage of Pacific mackerel in deliveries of mixed species (i.e., mixed with jack mackerel, *Trachurus symmetricus*; and Pacific sardine, *Sardinops caerulea*), the records are reasonably correct with a slight bias toward underestimation of actual poundage landed.

Catch statistics on Mexican commercial landings are incomplete. Landings from 1962 to 1969 were furnished by the Instituto Nacional de Pesca (INP) of Mexico, filling in the information for a critical period in the fishery. Earlier data on Mexican landings (Blunt and Parrish, 1969, Table 2) were reported as annual rather than seasonal catch, and for the years 1946 through 1953, and 1957 through 1970 Pacific and jack mackerel were undifferentiated. The latter problem was resolved by considering Pacific mackerel to be a constant fraction of the combined landings. Based on the years 1954–1956 and 1961–1963, this fraction is 0.611, with a high value of 0.958 (1954) and a low value of 0.457 (1963). Since combined Mexican landings were small for the years in which the problem exists, errors in estimation of Pacific mackerel landings will be small relative to total landings of all fisheries combined. A more difficult problem is the conversion of annual landings to season landings. As information on monthly catches is unavailable, we assumed the distribution of monthly catch of the Mexican fishery to be identical to that for the California fishery for the same year. Based on these proportions, annual catches were divided into estimated catches from January through April, and May through December, and were re-combined as season catches. Values prior to 1955 (except for 1947) were changed very little since about 95% of the annual California catch was made later than April. In later years this value was less, reaching a low of 70% in 1958.

Sport fishing landings were inconsequential prior to 1970, however, they have been included to complete the record. The California partyboat fleet has reported catches of all species since 1947 (Young, 1969). The partyboat fishery accounts for the majority of sport-caught mackerel. The total of all other segments of the sport fishery combined may roughly equal the partyboat catch (Pinkas, Thomas and Hanson, 1967; Pinkas, Oliphant and Haugen, 1968; unpublished data). Therefore the total sport catch was estimated to be twice the reported partyboat catch. All fish were assumed to weigh one pound when estimating landings in weight.

AGE COMPOSITION

Age composition of the California commercial landings since 1939 have been published (Fitch, 1951, 1953a, 1953b, 1955, 1956, 1958; Hyatt 1960; Parrish and Knaggs, 1971, 1972; Knaggs, 1972). Mexican commercial landings, the sport catch, and late reports from the California commercial fishery lack age composition information, making it necessary to assume that these catches had the same age composition as the published data. Total landings by age were estimated for each season by increasing each value by the season ratio of total catch of all fisheries to total catch used in the corresponding age composition article. Total pounds catch used in age composition articles was not documented for the 1939–40 through

1951–52 seasons, as the poundage for age 6+ fish was omitted and total poundage was not recorded. For seasons 1941–42 through 1948–49, the missing information was recovered from the original worksheets. For the remaining five seasons, 1939–40, 1940–41, and 1949–50 through 1951–52, the estimated number of age 6+ fish (corresponding to a mean length of 38.5 cm) gave estimated weights for this age group. From this the total weight of the aged landings was estimated and the appropriated proportion of increase could be derived (Table 3).

TABLE 3. Pacific Mackerel Ratios of Total Catch to Aged Catch (Weights in 1000 lb)

Season	*Age composition ages 0–5*	*Reports age 6+*	*Estimated total from age composition*	*Total all fisheries*	*Increase factor*
1939–40	82783	9760 *	92543	100161	1.0823
1940–41	100864	2646 *	103510	107755	1.0410
1941–42	65105	1054	66159	71855	1.0861
1942–43	43621	469	44090	48320	1.0959
1943–44	69552	597	70149	77904	1.1106
1944–45	75199	715	75914	80886	1.0655
1945–46	46532	2339	48871	52103	1.0661
1946–47	50533	3887	54420	60833	1.1173
1947–48	32709	2303	35012	42707	1.2198
1948–49	35245	503	35748	39744	1.1118
1949–50	46800	491 *	47191	53232	1.1256
1950–51	31617	224 *	31841	38410	1.2090
1951–52	31037	246 *	31283	34910	1.1159
1952–53	18691	71	18762	22692	1.2095
1953–54	6857	756	7613	11546	1.5166
1954–55	26656	63	26719	40364	1.5107
1955–56	26656	230	26756	48800	1.8239
1956–57	57128	0	57128	81070	1.4191
1957–58	54843	1345	56188	61027	1.0861
1958–59			24776	26040	1.0510
1959–60			41282	42552	1.0308
1960–61			39074	45805	1.1723
1961–62			44192	57678	1.3052
1962–63			45252	52612	1.1626
1963–64			34210	52066	1.5220
1964–65			24875	44076	1.7719
1965–66			7589	24681	3.2522
1966–67			4075	16147	3.9625
1967–68			1381	3689	2.6713
1968–69			3289	3689	1.1198
1969–70			1439	2466	1.7137

* Estimated by assumed weight of age 6+ fish.

The period before 1939 presents special problems, as no refined data have been published. Some otolith readings were made by D. Fry for the 1933–34 and 1934–35 seasons (unpublished), and length frequencies were taken regularly starting in 1929 (unpublished). A comparison of the early otolith readings with those in Fitch (1951) shows that lengths-at-age are consistent (Table 4). The samples appear to be occasional entire clusters of fish which were selected for usual length frequency measurements, and are therefore presumably unbiased.

TABLE 4. Validation of Unpublished Otolith Readings.

	Mean length-at-age *							
	Unpublished readings				*Fitch (1951)*			
	1933		*1934*		*1939–40*		*1940–41*	
Age	*n*	*L*	*n*	*L*	*n*	*L*	*n*	*L*
0	0	–	0	–	26	101.2	56	99.7
1	13	113.5	19	105.3	335	109.3	323	111.1
2	84	123.6	221	121.6	342	122.5	1040	120.2
3	130	130.6	159	130.7	486	131.5	483	130.0
4	115	137.4	192	139.9	160	141.1	298	136.9
5	37	148.9	125	143.8	91	147.8	44	145.0
6+	21	154.3	49	151.1	84	154.5	14	151.6

* σ_L is approximately 5.0 for all ages.

A reconstruction of the age structure of the landings from 1929–30 through 1939–40 was made by separating length frequencies into component normal curves. This was first attempted by Tomlinson (unpublished MS) using the computer program NORMSEP which he modified for the purpose. Tomlinson's modifications (Abramson, 1971) tend to introduce some bias into the estimating procedure, but increase the consistency of the estimated mean lengths-at-age with those from otolith readings, and thus presumably increase the accuracy of the percentage compositions estimated from the samples. Comparison of age composition estimated from length frequency with age compositions estimated from otolith readings is shown for 1933–34, 1934–35, and 1939–40 (Table 5). *NORMSEP* estimates show general agreement with overall age distribution, but estimates of landings for individual age groups may be considerably different. The 1933–34 season, in which the fewest otolith samples were examined (5 clusters with a total of 400 otoliths) shows the poorest agreement, particularly in ages 2 and 5. The other two seasons show remarkably good agreement in view of the fact that *NORMSEP* estimates do not stratify the

TABLE 5. Comparison of Estimated Age Composition of Early Pacific Mackerel Catches by NORMSEP and by Otolith Readings.
(1000 fish)

Season	*Otolith sample size*	*0*	*1*	*2*	*3*	*4*	*5*	*6+*	*Total*
1933–34									
Otoliths	400	0	3746	15419	25754	18943	6711	3446	74119
NORMSEP		0	2517	5511	21843	18560	16969	8721	74120
1934–35									
Otoliths	765	0	3369	36726	24504	28090	16675	6075	115438
NORMSEP		0	2199	35238	33004	21332	19086	4577	115436
1939–40									
Fitch (1951)	1524	2960	25200	26540	35130	10570	5340	6100	111840
NORMSEP		6431	23621	19729	34603	16597	3858	7001	111940

landings by time period as do the otolith-based estimates (Fitch, 1951[1]). Moreover, no consistent bias in age structure is apparent in the *NORMSEP* estimates except for a possible tendency to overestimate weak age groups which are surrounded by more numerous age groups, as in the estimate for age 3 in 1934–35. Due to the importance of the 1930's in the history of the Pacific mackerel fishery, and the desirability of obtaining an analysis of this period, the NORMSEP estimates of age composition will be used with the reservations necessary in interpreting analyses based on such unreliable data. The age compositions for 1933–34 and 1934–35 which were calculated from D. Fry's otolith readings are retained as being more reliable than the *NORMSEP* estimates. Catches by age and season are given in Table 6.

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[1] The description of the weighting procedure in Fitch (1951) is partially in error. Age sampling was stratified by length category and, as Fitch states, the otoliths read do not represent a random sample. Age frequency was not calculated as shown in his Table 19. The actual procedure used was similar to the stratified sampling plan of AGECOM (Abramson, 1971), wherein the number of fish observed in each length stratum is taken into account.

TABLE 6. Catches by Age and Season (1000 fish)

Season	*0*	*1*	*2*	*3*	*4*	*5*	*6 +*	*Total*
1929–30 *	26	11469	20724	19204	4804	3574	4592	64396
1930–31 *		1224	6296	4252	1684	589	60	14105
1931–32 *		848	8851	5484	1158	667	512	17520
1932–33 *		130	2899	5259	1254	846	685	11073
1933–34		3746	15419	25854	18943	6711	3446	73669
1934–35		3369	36726	24504	28090	10675	6074	109438
1935–36 *		7621	8929	43255	44738	23577	6771	134891
1936–37 *		1705	15477	13198	25079	26669	6201	88329
1937–38 *	137	1273	2236	6931	13724	22451	10560	57322
1938–39 *	2058	11036	30473	15755	4108	10375	9805	83610
1939–40	3204	27274	28724	38021	11440	5779	6602	121044
1940–41	2408	21646	72164	26297	14107	1502	1722	115792
1941–42	432	13584	28732	27870	5562	1054	596	77830
1942–43		32193	10087	13916	5776	901	285	63158
1943–44	928	13840	60090	11279	7922	1202	438	95699
1944–45		17640	20295	36126	8217	1722	473	84473
1945–46	593	15247	11010	10937	10994	3548	1565	53894
1946–47	626	10429	28865	13271	5210	2564	2802	63767
1947–48	8759	1680	9734	13348	6205	2463	1892	44081
1948–49	1180	70410	3530	841	1229	477	325	77992
1949–50	153	24558	55441	4816	774	657	346	86745
1950–51	7	4659	23247	19134	1133	87	169	48436
1951–52	858	1766	4941	15479	12417	243	172	35876
1952–53	104	56	630	1555	11471	3333	40	17189
1953–54	18559	1025	720	884	244	557	593	22582
1954–55	852	60482	5881	314	107	0	59	67695
1955–56	7728	6497	38586	10980	372	27	232	64422
1956–57	30	70145	21252	20777	5167	88	0	117459
1957–58	1505	6764	33112	12308	8863	2500	1100	66152
1958–59	17304	1342	6217	11419	3671	1182	306	41441
1959–60	1595	58544	4341	1082	1323	432	143	67460

1960–61	2928	20726	23316	9004	2354	487	302	59117
1961–62	23490	33441	17054	12158	2556	268	90	89057
1962–63	60	30235	13936	10056	3867	398	41	58593
1963–64	67	3840	22285	12945	7899	1071	137	48244
1964–65	140	7006	5410	10210	13527	1740	152	38195
1965–66	12976	1255	761	1688	5483	8612	1551	32326
1966–67	2627	7453	1438	1106	935	2512	1569	17640
1967–68	7656	363	254	270	158	85	134	17640
1968–69	7069	548	204	356	86	81	122	8920
1969–70	14	2641	470	74	84	81	14	3378

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* Age composition estimated from length frequency. These data are unreliable.

POPULATION BIOLOGY

GROWTH

A very large amount of data is published on the age composition of the southern California catch of Pacific mackerel. Annual growth in length is also well documented. However, documentation is lacking on the seasonality of growth and on growth in weight generally. Individual weights were not recorded for the market samples until the mid 1960's. In addition published age-composition data represent a composite of information for the entire season.

Von Bertalanffy growth equations and length-weight relationships were calculated by Knaggs and Parrish (1973) for data from the 1958–1959 to 1969–70 seasons. They reported that there were no significant differences at the 1% level between their data and Fry's (1936b) data. They also reported little correlation between 29 years of estimates of recruit abundance and mean size at age 1 ($r = -0.208$). However, it should be noted that a good comparison (i.e., weight at a given age) is lacking. In this instance mean size at age 1 is the mean length of fish sampled during the season (i.e. May 1–April 30) and this mean age may differ from year to year due to availability or seasonal variations in fishing pressure.

The growth estimates used in the present paper are from the von Bertalanffy growth equation and the length-weight relationship given by Knaggs and Parrish (1973). Both annual growth and weight at capture were used in simulation models (Table 7). Weight at the beginning of the season (May) was used to calculate spawning biomass and annual growth.

TABLE 7. Length [1] and Weight [2] By Age of Pacific Mackerel (From Knaggs and Parrish 1973)

			At beginning of season (Birthday)		*At capture*	
Age		*t*	*Length*	*Weight*	*Length*	*Weight*
1	May	0.5	252 mm.	192 gms.		
	Oct.	1.0			273 mm.	253 gms.
2	May	1.5	292	317		
	Oct.	2.0			308	382
3	May	2.5	323	448		
	Oct.	3.0			336	512
4	May	3.5	348	574		
	Oct.	4.0			358	633
5	May	4.5	367	689		
	Oct.	5.0			375	741
6	May	5.5	382	789		
	Oct.	6.0			388	834

[1] $L_t = 436.12\,(1 - e^{-0.24444\,(t + 3.0222)})$

[2] $W = 0.000001366\,L^{3.39358}$

Weight at capture (October) was used to calculate catch. Length at the first birthday (May), with the von Bertalanffy equation as fitted by Knaggs and Parrish (1973), is calculated with t = 0.5 and the length of age 1 fish at capture is calculated with t = 1.0. This correction is necessary due to the fact that the von Bertalanffy equation was calculated with the criteria for age 1 being all fish between the ages of 1 and 2. The von Bertalanffy estimate with t = 1.0, therefore, is an estimate of length at an age of 1.5 years.

REPRODUCTION

Age at maturity and percent spawning by age group were not well documented during the early fishery. According to Fry (1936b) "the yearling fish do not spawn whereas most of the two-year-olds do." Fitch (1951) stated that most mackerel do not spawn until their third or fourth year (i.e., age 2 or 3). For the period of 1958–70 Knaggs and Parrish (1973) found that 22.5%, 65.7%, 75.1%, 84.7%, 84.2% and 87.0% of age group 1 through 6+ females sampled during the period of April–August were mature or maturing.

The above figures represent minimum percentage maturity of female fish, as early spawners might have completed spawning when captured in August or late spawners might be immature when captured in May. Therefore, in the present work we have decided to assume that 100% of the fish of age 4 or older are mature. The percentages mature of ages 1, 2, and 3 were increased by the same proportion as ages 4+ (i.e., 0.17). This results in percentages of 26%, 77%, and 88% for ages 1, 2, and 3 females.

Males apparently mature at a slightly younger age than females (Klingbeil, Calif. Dept. Fish and Game, personal communication). However, only the proportion of female fish are considered in measuring spawning biomass, with the assumption that males spawn in the same proportion as females. The fact that egg and larva surveys are used to measure biomass is the primary reason for this assumption Such surveys are capable of measuring spawning products of female fish only. A second reason is that the true reproductive potential of a pelagic fish population is measured by that segment which produces eggs (i.e., females), given the condition that fertilization is efficient over a wide range of male to female abundance ratios.

The major inconsistency between the data taken in the early fishery, when biomass levels were high, and the late fishery, when biomass levels were low, is the percentage of age 1 fish that spawn. The Fry (1936b) and Fitch (1951) data were taken when biomass was high. The percentages mature reported by Knaggs and Parrish (1973) are average values taken over the period 1958–1959 to 1969–1970, when biomass varied from moderately high to very low levels. In an attempt to determine if the percentage of age 1 fish spawning depends on density, the original market samples used by Knaggs and Parrish (1973) were analyzed to see if a pattern could be determined. Maturity stages were not recorded in market samples prior to 1958–1959, and in individual samples these data were sometimes missing for several years thereafter. When analyzed by individual year the numbers became so small that validity was questionable. However, during the period 1969–1971, when the spawning biomass was at extremely low levels and large numbers of age 1 fish were sampled, 50% of the age group 1 fish were mature or maturing.

The available information suggests that there is an inversely density-dependent relationship between population size and the percentage of age 1 fish that spawn, although the exact form of this relationship is difficult to demonstrate. It appears that the percentage of age 1 spawners can be approximated at three general biomass levels. An exponential curve fitted to these points gives the following relationship, which was used in the regressions to determine recruit-spawner functions and in all simulations. (Figure 2)

$$PS = 0.540\ e^{-0.00717\ TPOP}$$

where PS = proportion of age 1 fish spawning
TPOP = total population biomass in millions of pounds

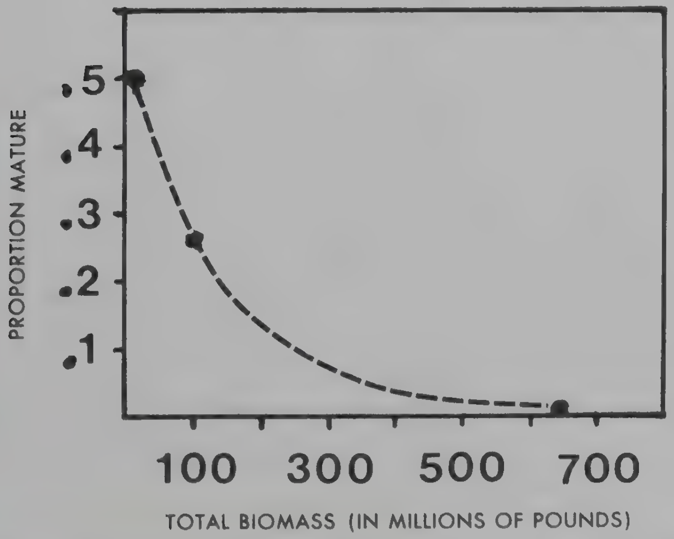

FIGURE 2. The relationship between total biomass and the proportion of age 1 spawners

There is a hypothesis other than density dependence to explain the increasing percentage of age 1 fish that spawn at low biomass levels. Fry (1936b) stated that a small proportion of fish in the southern Baja California stock spawned at age 1. It is possible that a small number of fish from the southern Baja California stock enter the California fishery. These fish could provide an increasing proportion of the mackerel available to the California fishery as the northern stock declined to the very low levels of the late 1960's. Tagging studies neither confirm nor invalidate this alternate hypothesis, because fish south of central Baja California were not tagged during the major tagging work carried out by Fry and Roedel (1949) or in more recent work (Knaggs 1974).

The eggs and larvae of Pacific mackerel are pelagic. The eggs hatch approximately three days after fertilization, depending on temperature (Fry 1936a). Fry (1936b) found that most of the eggs were spawned in water less than 88 m deep and between 16.7 and 20.6C (62 and 69°F). Ahlstrom (1959) suggests that spawning occurs closer to the shore and closer to the surface in Pacific mackerel than in the other major pelagic species in the California Current region. Kramer (1969) reported that the abundance of Pacific mackerel eggs fell off sharply below 23 m. Estimates of fecundity in Pacific mackerel are based on relatively few individuals. MacGregor (1966) reported that the Pacific mackerel produces 304 eggs per gram of fish (based on counts for six specimens). MacGregor (1975) reported that 18 Pacific mackerel averaged 259 eggs per gram. He suggested that a lower estimate of fecundity per body weight was associated with first-time spawners in a number of species but he did not report that this occurs in Pacific mackerel.

Fry (1936a) found that Pacific mackerel eggs varied in size during the spawning season; eggs were larger in April-May than in June-July. The data on age at maturity reported by Knaggs and Parrish (1973) showed that spawning of older mackerel peaks in May while in age 2 it peaks in June and in age 1 it peaks in July. Bakun (1973) shows that peak upwelling in central Baja California occurs in May. This suggests that older fish produce larger eggs that are hatched during the period of peak upwelling in central Baja California and that the smaller eggs from younger fish hatch after the normal peak of upwelling. Thus the alteration of the age structure of the population by fishing could result in a reduction of average spawning success and an increase in the variance if upwelling is vital to larval survival. The larvae of younger fish could have a shorter period before starvation would occur. This could be caused by less caloric yolk reserves or a higher metabolic rate due to the higher temperatures they would encounter later in the season. Hempel (1965) suggests that the above considerations affect survival of Norwegian herring.

The distribution of Pacific mackerel larvae is considerably wider than that of the eggs. Principal concentrations are often well offshore and undoubtedly are heavily controlled by transport and convergence patterns. Most larvae have been taken off of central Baja California in the region near Punta Eugenia (Figure 3).

SCHOOLING

Schooling behavior in the California Pacific mackerel stock is not well documented in the literature. Sette (1943), in discussing Atlantic mackerel (*Scomber scombrus*), reported that fish-of-the-year school separately from the rest. Yearlings usually school separately but may join schools of adults, especially when the adults are predominantly 2-year-olds. The adults, age 2+, travel in mixed schools. Sette attributed the above schooling by age to the fact that the larger, older fish tend to have a higher cruising speed than smaller fish. The age composition of market samples of Pacific mackerel caught off of California suggests that this same pattern is also found in Pacific mackerel. Yearling Pacific mackerel are often found

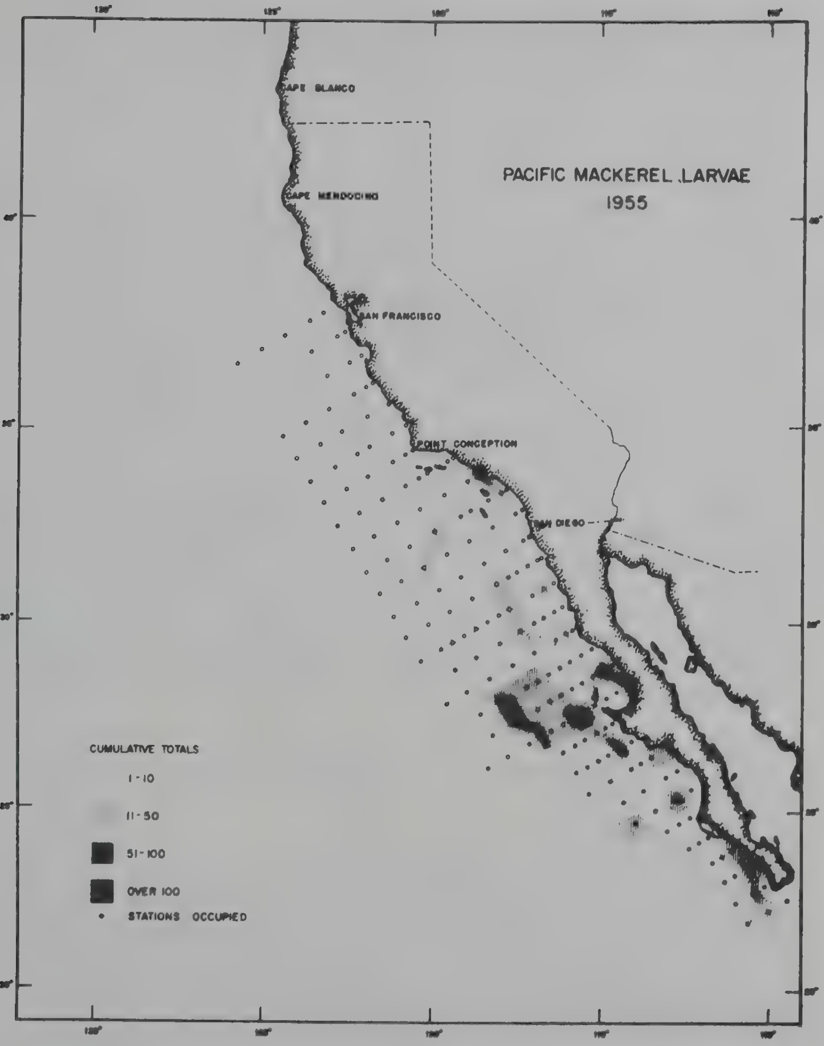
CAPE BLANCO
CAPE MENDOCINO
PACIFIC MACKEREL LARVAE
1955
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
CUMULATIVE TOTALS
1-10
11-50
51-100
OVER 100
STATIONS OCCUPIED

FIGURE 3. **Distribution and relative abundance of Pacific mackerel larvae in 1955 (fig. 20 of Kramer, 1960)**

schooling with immature jack mackerel (*Trachurus symmetricus*) which tend to have a lower cruising speed than adult Pacific mackerel. Early management policies favored by members of the canning industry reflected an awareness of this pattern, as they were largely concerned with limiting the catch of young-of-the-year and yearling fish. It therefore appears that size restrictions could be effective in preventing the capture of young-of-the-year mackerel, and to a lesser extent yearlings. Restrictions at sizes or ages larger than this are not feasible in the purse-seine fishery due to mixed schooling.

NATURAL MORTALITY RATE

As in most fishery analyses, the rate of natural mortality (M) will be assumed to be constant for lack of better information. The most direct measure of M for the Pacific mackerel was made by analysis of the number of tags returned from fish released in southern California waters (Fry and Roedel, 1949). Estimates of M ranging from 1.1 to 1.3 were obtained depending on method of analysis and assumptions of tagging mortality rates. These estimates are very high, corresponding to loss of 70 percent per year, and are inconsistent with age frequency in the catches particularly for the early years of the fishery when older fish were common. Fry and Roedel concluded that tagging experiments did not supply realistic values of natural mortality rates for the Pacific mackerel.

Another source of mortality rate information is length frequency data taken in the very early period of the fishery. Length frequencies were first taken in the 1929–30 season, the second season of significantly large landings (cf. Figure 1). Comparison of 1929–30 with 1930–31 length frequency (Figure 4) shows a more rapid decrease in abundance of larger fish in the latter season, suggesting an increase in total mortality. A bulge in the 1929–30 graph involving 36 to 41 cm fish suggests large recruitment in the mid 1920's and will cause an underestimate of the mortality rate. This bulge disappeared in the length frequency for the following 1930–31 season.

Beverton and Holt (1956) showed that the total mortality rate (Z) can be estimated from length frequency information if von Bertalanffy growth constants are available:

$$Z = [K(L_{\infty} - \overline{L})]/(\overline{L} - L^1]$$

where L^1 is the smallest length fully represented (or lower cut-off point) and $\overline{L}$ is mean length of fish L^1 or longer. K and L_{∞} are the von Bertalanffy growth constants. Pacific mackerel appear to show different relative growth rates for different years, possibly an effect of varying population size (Knaggs and Parrish 1973). Von Bertalanffy growth constants were calculated from length and age data taken in 1933–34 and 1934–35, the closest available data to the time period under consideration (Table 5). Using the method of regressing annual growth increment on initial length (Figure 5), the X-intercept is an estimate of L_{∞} and the slope is a function of K (Gulland 1969). In order to avoid effects of uneven recruitment on the catch curve analysis, L^1 was increased the equivalent of a year's growth by the relationship

$$L_{t+1} = L_{\infty}[1 - e^{-K}(1 - [L_t/L_{\infty}])]$$

which is derived from the von Bertalanffy growth equation. Thus we obtain total mortality rates for approximately the same cohort of fish in the two seasons. The Beverton and Holt equation gives a Z of 0.317 for the 1929–30 catch curve, and a Z of 0.424 for the 1930–31 catch curve (Table

8). As discussed previously, these values are probably biased and represent low estimates; however, the values imply a natural mortality rate much lower than those obtained from the mark-recapture data. Since the Pacific mackerel had undergone only one full season of fishing in addition to the season underway in 1929–30, a natural mortality rate of 0.3 to 0.5 is consistent with these data.

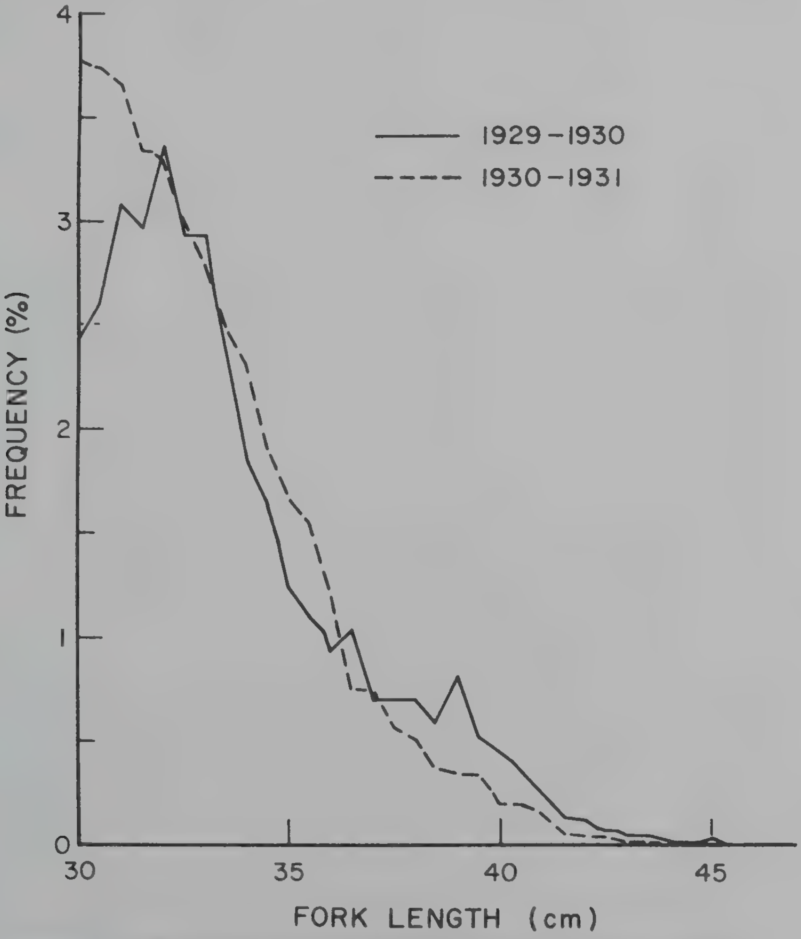

FIGURE 4. Pacific mackerel comparison of length frequency for 1929–30 and 1930–31

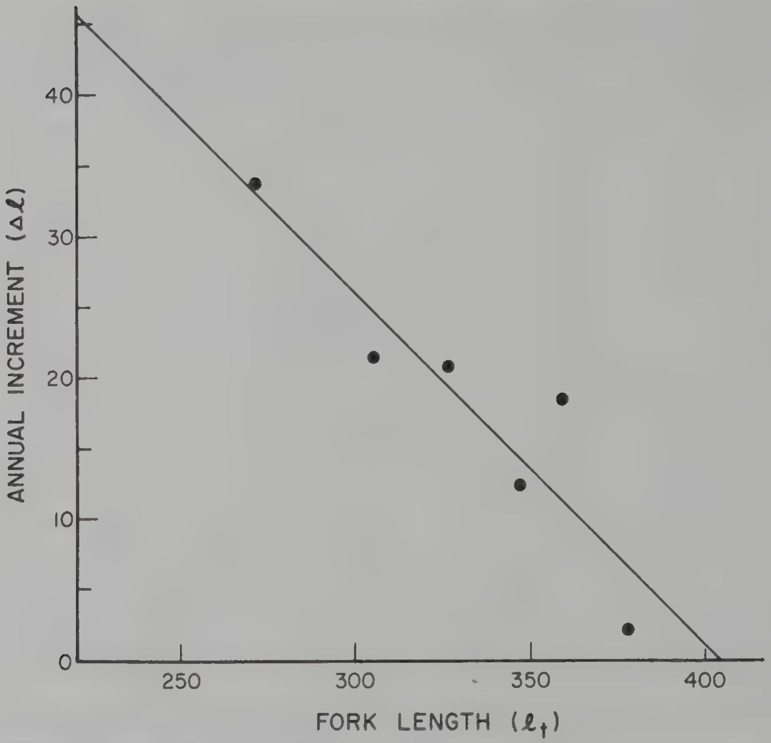

FIGURE 5. **Pacific mackerel von Bertalanffy growth curve parameter estimation. Data from D.H. Fry otolith readings 1933–1934.**

A final method of estimating the rate of natural mortality involves the y-intercept of the regression of total mortality rate upon effort. Since M is being estimated for use in cohort analysis, and the estimates of total mortality rate in this procedure are derived from cohort analysis, it may appear circular. Actually it is not circular, since in cohort analysis errors in M result in counterbalancing errors in estimated F. Z is relatively unaffected making an iterative solution appropriate.

Table 8. Catch Curve Estimates of Total Mortality Rates from Length Frequency and Von Bertalanffy Growth Curve (L_∞ = 404.6 mm, K = 0.221).

Season	*n*	$\bar{L}$	$\bar{L}$	*Z*
1929–30	346	337.5	365.05	0.317
1930–31	317	350.0	368.70	0.424

Direct effort estimates for Pacific mackerel are not available, but a relative effort measure can be obtained from the night-light survey data collected by the California Department of Fish and Game sea surveys in the fall of the years 1950 to 1961 (Mais 1974). An abundance index was calculated as the percent of night-light stations at which Pacific mackerel were observed (Table 9). The geographic area covered by the survey is Ensenada to Point Conception. This abundance index can be used to derive an effort index (f). If the abundance index (I) is related to true mean abundance ($\overline{N}$) by some constant c,

$$\overline{N} = cI$$

and instantaneous fishing mortality (F) is related to catch and mean abundance by

$$F = (C/\overline{N})$$

a measure of nominal effort (f) which is proportional to F is obtained by:

$$f = cF = (C/I)$$

Estimates of f obtained by this method, and estimates of Z from a cohort analysis using $M = 0.5$ are given in Table 9. The regression of Z upon estimated f gives an M estimate of 0.95, while the regression of f upon Z gives $M = 0.32$ (Figure 6). The variance of the effort estimate relative to the variance of the Z estimate is quite large, due to the crude method of estimation and small sample size, so the latter regression is to be favored (Ricker 1973). The Z-intercept estimate of M would therefore fall between 0.4 and 0.6. Since $M = 0.5$ was used in the cohort analysis, this value of M is consistent with the data.

Table 9. Abundance Index, Effort Index and Total Mortality Rate Estimates for Pacific Mackerel.

Season	*Night-light abundance index (% occurrence)*	*Total catch (1000 lb.)*	*Effort index (f)*	*Total mortality rate (M = 0.5)*
1950–51	17.3	38497	2225	1.363
1951–52	8.8	34910	3967	1.604
1952–53	2.6	22692	8728	2.397
1953–54	0	11546	—	1.839
1954–55	23.4	40364	1725	0.729
1955–56	12.3	48800	3967	1.528
1956–57	15.2	81070	5334	1.046
1957–58	6.7	61027	9109	2.056
1958–59	3.9	26040	6677	1.854
1959–60	18.9	42552	2252	1.276
1960–61	11.7	45805	3915	2.019
1961–62	7.2	57678	8011	1.636

A last source of information on probable values of M results from comparing relationships between population parameter values and rate of natural mortality in other species. Beverton (1963) shows the relationship of M to the maximum age observed (Tmax) for a number of different species. The oldest Pacific mackerel which has been observed was 11 years of age (Fitch 1951) suggesting a probable range of M from 0.3 to 0.7.

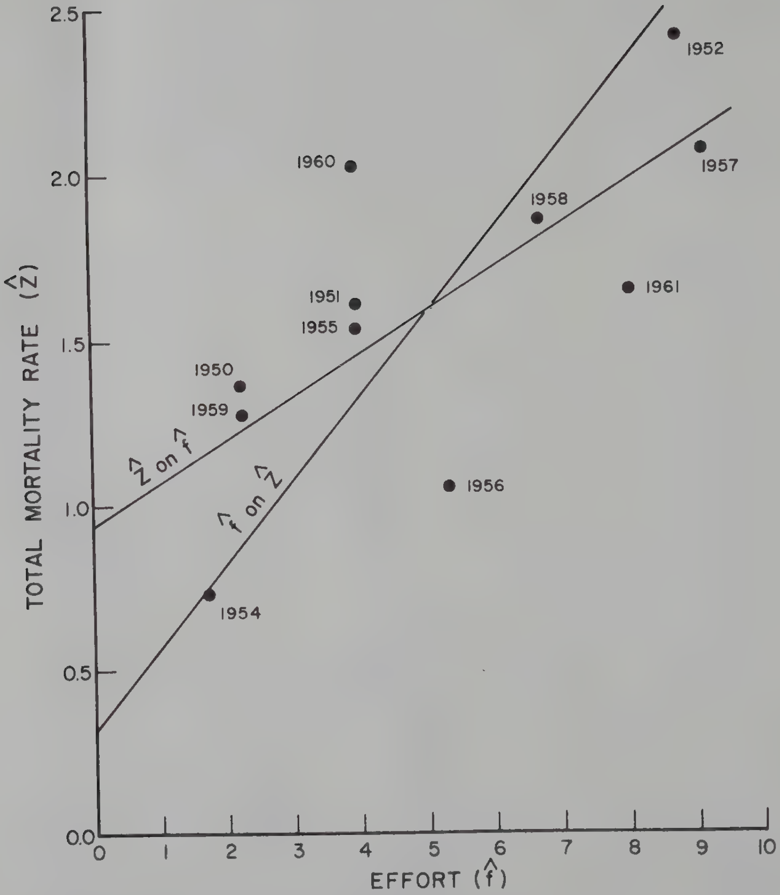

FIGURE 6. Estimation of M by the relationship of Z to F.

Another comparison can be made between the von Bertalanffy parameter K, and M, as shown in Beverton and Holt (1959). Values for K of 0.244 (Knaggs and Parrish 1973) for recent years, and of 0.221 for earlier years as estimated above, suggest an M of 0.4 to 0.6 when compared with similar values for other free-swimming large species of fish (Beverton and Holt 1959). Estimates of M from comparative studies such as these are of poor reliability, but do give support to the other estimates.

Comparision of estimates of the rate of natural mortality is obtained by various methods (Table 10), suggests that M is probably in the range of

0.4 to 0.6, with the most consistent single value being M = 0.5. This value will be used throughout the rest of the analysis.

Table 10. Estimates of Natural Mortality Rate for Pacific Mackerel

Natural mortality rate estimate M	*Source*	*Comment*
1.1–1.3	Tagging (Fry and Roedel, 1949)	Unreliable, probably overestimated.
0.3–0.5	Early catch curves	Subject to unknown bias from uneven recruitment
0.5	Regression of Z on f	Probably the best estimate available; estimate is dependent on unknown variances.
0.3–0.7	Comparative studies	Tmax = 11 years; method is unreliable.
0.4–0.6	Comparative studies	K = 0.22, 0.24; method is unreliable

COHORT ANALYSIS

ESTIMATION OF FISHING MORTALITY RATES

Fishing mortality rates were estimated using the method of cohort analysis first developed by Murphy (1965, 1966) and generalized by Tomlinson (1970). A "backward" solution was chosen due to its properties of convergence: a wide range of fishing mortality rate estimates for the oldest or most recent age group gives a progressively narrower range of variation in estimates of F for younger age groups or earlier seasons. A constant rate of natural mortality ($M = 0.5$) was assumed. All fish of age 4 and older were assumed to be fully recruited. This assumption was warranted by trial solutions using older ages at assumed full recruitment. Also, sample sizes of older fish are often very small and highly variable.

Two methods of determining seasonal estimates of F for fully recruited fish were investigated. The first method is similar to that used by Murphy (1966) for sardines. The cohort of fish consisting of those fish of age 4+ is the same cohort as those fish age 5+ in the succeeding season. In the same season, 4+ and 5+ cohorts are presumably fished at the same rate, as they are assumed to be fully recruited. Thus the fishing mortality rate for the age 5+ fish can be used to estimate the fishing mortality rate for the age 4+ fish of the preceding season by cohort analysis using the catch ratio of age 5+ to age 4+ fish. The mortality rate estimated for the age 4+ fish can then be assigned to the age 5+ fish in the same season as input to the next preceding season, and the backward solution of seasonal fishing mortality rates continues in stepwise fashion.

An alternative method was tried, which does not combine age groups of fish, but more fully utilizes the property that all fully recruited age groups are assumed to be equally exploited in a fishing season. The fishing mortality rates form a matrix with rows of year-classes (cohorts) and columns of ages, so that diagonals represent fishing seasons. An iterative procedure was used to obtain values of F for all cells which minimize an overall weighted sum of squares of deviations with respect to the season means.

The first method considers seasons in pairwise fashion only, so that errors in fishing mortality rate estimates are passed on to the next season's estimate (with convergence reducing their magnitude). The second method connects several year-classes and seasons, with varying degrees of freedom due to the convergence property. Consider a single year-class for which trial fishing mortality rates have been determined by cohort analysis. F for the youngest age group will vary little for a wide range of F of the oldest group. Each age group is contributing to the sum of squares for its respective season, so the mean fishing mortality rate of the earliest season tends to be anchored by the least variable F of the youngest age group while F of the oldest age group is relatively free to assume a value which is most consistent with its season mean. Convergence of the backwards time series is still a basic property of the second method, although linkage involves every year-class which was fished in any season in which the year-class under consideration was fished, rather than the simple pairwise linkage of the first procedure. This linkage system gives the second method greater stability with respect to propagated errors, at a sacrifice of sample size. The respective advantages and disadvantages of the two methods require more extensive and quantitative examination than they have received here. In practice the two methods give very similar results, although the second method may vary in sensitivity over different portions of the time series, sensitivity goes undetected in the first method. Due to the unknown biases of the second method, and the general agreement with estimates made by the simpler first method the first method was used for this analysis.

No independent estimate of the fishing mortality rate (F) for the recent portion of the time series is available, making it necessary to use a reasonable guess as a starting value. Alternative trial values of 0.5, 1.0 and 1.5 for 1969–70 were compared (Table 11), and convergence resulted in little difference for the 1966–67 season and earlier. The intermediate value, F = 1.0, is used as an arbitrary starting value for solution of the time series. For younger age groups, the starting value for 1967–70 was modified by arbitrary recruitment factors to give F(age 3) = 1.0, F(age 2) = 0.75, F(age 1) = 0.50, and F(age 0) = 0.25, which were used to initiate cohort analysis of these year-classes. These estimates do not contribute to the general solution, and were made only to fill out the time series with estimates for recent seasons.

TABLE 11. Comparison of the Effect of Different Assumed Values of F for the 1969–70 Season on the Time Series of Fishing Mortality Rate Estimates for Fully Recruited Fish.

Season	*Estimated fishing mortality rate*		
1969–70	0.5	1.0	1.5
1968–69	0.547	0.781	0.906
1967–68	0.390	0.481	0.519
1966–67	1.651	1.800	1.847

The three trial solutions shown in Table 11 demonstrate a general rule in the behavior of cohort analysis: large values of F converge more rapidly than do small values of F. Use of cohort analysis on simulated catch data shows that in the backward solution the rate of convergence (percent approach to true F per iteration, relative to the error in the preceding F estimate) increases as F increases, and is zero at F = 0 (Table 12). A forward solution will show similar rates of divergence, estimates of F will approach progressively either zero or infinity, leading to an unrealistic solution of the time series.

The cohort analysis solution of the time series of catches by age is given in Table 13. The catches themselves are given in Table 6. A cohort analysis

TABLE 12. Approximate Rates of Convergence * for Cohort Analysis, Backward Solution, M = 0.5, as Determined by Simulated Catches.

F	*Rate of convergence*
0	0%
0.1	11%
0.2	19%
0.3	26%
0.5	39%
1.0	65%
1.5	78%
2.0	85%

* Approximate rate of convergence is 100% $(F_{i-1}-F_{i-1})/F_i-F_i)$ when $F_{i-1} = F_i$, and F_i is near F. Convergence becomes divergence in the forward solution.

of fishing mortality rates for the 1928–29 season was impossible due to lack of sampling. A rough guess of 0.2 was obtained by multiplying the 1929–30 F by the ratio of total catches for the two seasons. Approximate fishing mortality rates for the younger age groups were obtained by applying approximately the same relative recruitment ratios as in 1929–30. Fishing mortality rate estimates before 1939 are unreliable due to the aforementioned problems in estimating age composition. The estimates for 1928 through 1932–33 are particularly poor due to the lack of convergence at low fishing mortality rates.

As there were two independent fisheries for the Pacific mackerel, it is useful to separate fishing mortality rates into purse seine and scoop fleet components. This separation is done by multiplying the total fishing mortality rate (age 4 +) by the ratio of the fishery segment catch to total catch:

$$F\ (\text{scoop}) = [C\ (\text{scoop})/C\ (\text{total})]\ F\ (\text{total})$$

Scoop and striker catch were combined under the heading of "scoop" and purse-seine and "others" were combined under the heading of "purse seine" (Table 13). The "other" category amounts to a very small percentage of the catch. Catches by fishery segment were obtained from Roedel (1952) wherein values were given for 1939 through 1950, and estimates for the seasons before 1939 were presented graphically. More recent catches were compiled from source documents.

POPULATION ESTIMATES

The fishing mortality rates in Table 13 are combined with the catches in Table 6 to give population sizes for age groups at the beginning of the fishing season (i.e., on the "birthday"). The annual exploitation rate (E) is given by

$$E = (F/F+M)\ (1 - e^{-(F+M)}),$$

and initial population size is in numbers estimated by

$$N = C/E.$$

Population sizes in weight, or biomasses, are obtained by assigning the

TABLE 13. Fishing Mortality Rates By Season

Season	Age				4+ (Fully recruited)	Exploitation rate age 4+	Proportion catch by scoop	F purse seine & other	F scoop
	0	1	2	3					
1928–29	—	0	(0.10)	(0.15)	(0.20)	(0.144)	—	(0.2)	—
1929–30	—	.055	.162	.201	.330	.224	—	.330	—
1930–31	0	.003	.052	.062	.033	.026	—	.033	—
1931–32	0	.002	.032	.080	.029	.022	—	.029	—
1932–33	0	.0002	.010	.032	.032	.025	—	.032	—
1933–34	0	.007	.034	.159	.214	.153	.06	.201	.013
1934–35	0	.017	.120	.096	.366	.245	.10	.331	.035
1935–36	0	.092	.079	.282	.357	.240	.04	.344	.013
1936–37	0	.016	.385	.221	.371	.248	.06	.349	.022
1937–38	.001	.006	.035	.425	.542	.337	.13	.472	.070
1938–39	.005	.071	.252	.519	.715	.414	.20	.574	.141
1939–40	.110	.110	.371	.858	1.553	.655	.59	.622	.911
1940–41	.009	.132	.686	1.075	1.648	.678	.57	.711	.937
1941–42	.001	.091	.364	.969	1.115	.553	.63	.412	.703
1942–43	0	.105	.125	.431	.825	.457	.78	.181	.644
1943–44	.005	.125	.411	.278	.694	.405	.61	.268	.426
1944–45	0	.084	.382	.689	.482	.307	.77	.113	.369
1945–46	.011	.152	.233	.530	.689	.403	.70	.205	.484
1946–47	.013	.379	.698	.717	.783	.441	.52	.379	.404
1947–48	.018	.061	1.166	1.387	1.532	.655	.45	.835	.697
1948–49	.004	.275	.241	.392	.634	.379	.75	.160	.474
1949–50	.005	.166	.522	.911	1.223	.583	.57	.520	.703
1950–51	.001	.298	.328	.495	.963	.471	.43	.488	.375
1951–52	.108	.268	.897	.549	1.164	.550	.16	.978	.186
1952–53	.001	.012	.200	1.348	1.897	.719	03	.832	.065
1953–54	.049	.011	.301	.696	1.339	.612	.24	1.013	.326
1954–55	.005	.310	.110	.292	.229	.163	.49	.117	.112
1955–56	.029	.071	.479	.435	1.028	.526	.24	.780	.248
1956–57	.001	.553	.498	.768	.546	.338	.11	.487	.059
1957–58	.019	.232	.840	.929	1.556	.660	.25	.161	.395
1958–59	.064	.028	.496	1.326	1.354	.616	.44	.764	.590

1959–60	.007	.449	.165	.206	.776	.438	.54	.361	.415
1960–61	.007	.158	.465	.902	1.519	.652	.04	1.461	.058
1961–62	.105	.146	.264	.702	1.136	.559	.05	.080	.056
1962–63	.002	.265	.114	.346	.760	.432	01	.754	.006
1963–64	.003	.194	.456	.204	.748	.428	.02	731	.017
1964–65	.017	.761	.667	.570	.487	.310	.01	.480	.007
1965–66	.620	.290	.234	.670	1.096	.547	.02	1.074	.022
1966–67	.937	1.539	.966	.952	1.800	.704	—	1.800	—
1967–68	1 180	.447	.244	.711	.481	.306	—	.481	—
1968–69	494	.322	727	.966	781	.440	—	.781	—
1969–70	(.250)	(.500)	(.750)	(1.000)	(1.000)	(.518)	—	(1.000)	—

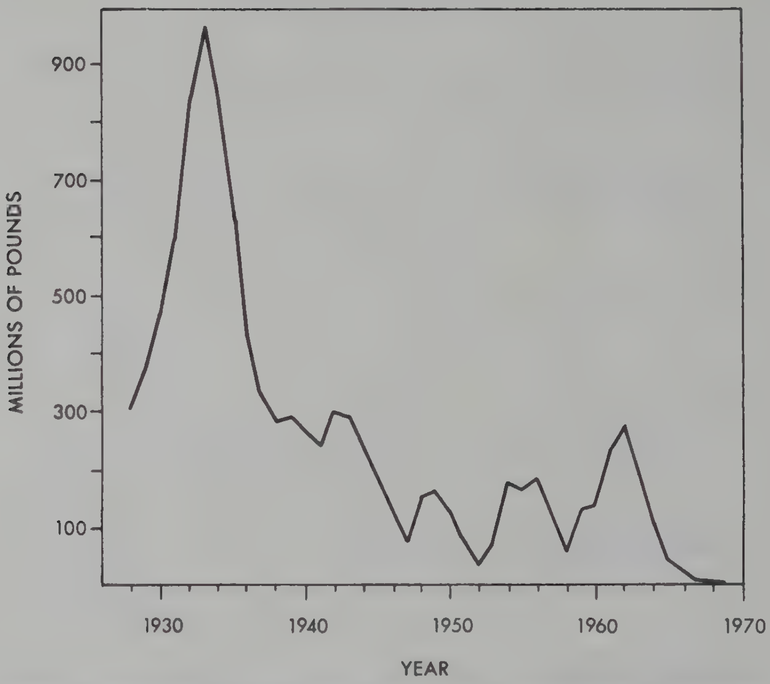

FIGURE 7. Total biomass of the California Current stock of Pacific mackerel (MacCall pers. comm.)

weights at age for May given in Table 7 to the populations estimated by the above equations. The resulting biomass estimates are given in Table 14. Total biomass (Figure 7) is estimated by summing the biomass of the individual age groups, not including age group 0. Spawning biomass is estimated in similar fashion, except that age group contributions are modified by the percentage of females which are capable of spawning (Figure 2).

RECRUITMENT AND SPAWNING SUCCESS

Recruit biomass (R), measured in weight at age 1, is given in Table 14. Spawning success has been highly variable, and there appears to be little density-dependent effect even on a logarithmic scale, when population biomasses are in their normal historical size range (Figure 8). However it appears that recruitment strength is much less variable when spawning biomass (P) is greater than 200 million pounds. All of the disastrously poor recruitments of 20 million pounds or less were produced by spawning biomasses less than 200 million pounds.

An index of spawning or reproductive success, as measured by ln(recruits/spawners) shows a somewhat cyclical pattern over time (Figure 9). The sequence of poor spawning successes that led to the collapse of the stock is remarkable both in its magnitude and its duration. Such a sequence of five consecutive spawning failures would have caused a drastic decline in abundance even in the absence of a fishery. However, harvest during and after the period undoubtedly retarded the subsequent recovery. Variability of spawning success during the period 1928 to 1945 was significantly ($P < 0.01$) less than during later years (Table 15). Three hypotheses are suggested as possible explanations for the increase in variance. First, the computations are somewhat unreliable up to the 1939 season, and the method of estimating early age compositions may have artificially reduced the variability. Second, key environmental factors in spawning success may have actually been more variable in the later period. The environmental conditions which influence reproductive success from a spawning event will be termed the "spawning environment". The

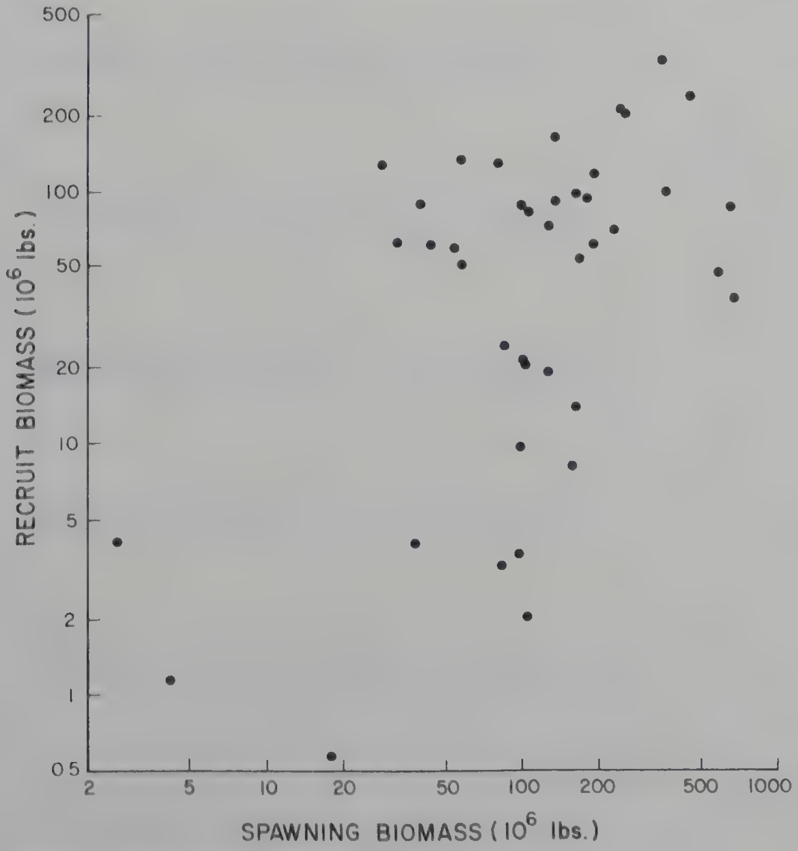

FIGURE 8. Spawner-recruit relationship

TABLE 14. Beginning Of The Season Biomass Estimates*
(In 1000 lb)

Year	*Age 1*	*Age 2*	*Age 3*	*Age 4*	*Age 5+*	*Total biomass*	*Spawning biomass*	*Age 1 recruit biomass of resulting year class*
1928	97124	144695	32843	30966	0	305628	177143	92640
1929	92640	104583	109226	22301	45179	373929	247553	199914
1930	199914	98300	72156	68522	31474	465866	239542	205552
1931	205552	214703	72230	53521	64945	610951	348739	321127
1932	321127	220947	168747	52596	76532	839949	448175	230089
1933	230089	345729	177479	128910	82379	964586	633805	84509
1934	84509	246033	271010	119406	115253	836211	622707	36925
1935	36924	89447	177079	194218	157021	654689	576125	46621
1936	46621	36259	67083	105396	164638	419997	358225	96014
1937	96014	49416	20022	42430	121672	329554	224652	69185
1938	69185	102801	38717	10332	60667	281702	189182	115438
1939	115438	69453	64410	18254	23563	291118	159706	96374
1940	96374	106873	37281	20322	6470	267320	149545	90387
1941	90387	80230	50977	12488	4506	238588	132451	159222
1942	159222	76545	44077	14454	3670	297968	126001	71999
1943	71999	136733	53936	25514	5341	290523	185444	60555
1944	60555	56351	84430	31904	9837	243077	165151	52797
1945	52797	49285	32546	32607	17573	184808	124346	18933
1946	18933	51286	30137	14301	16783	131440	101078	20308
1947	20308	13535	22294	11340	8941	76418	56661	130928
1948	130928	12780	3250	3946	3111	154015	43188	60814
1949	60814	92240	8205	1572	2410	165241	92269	9648
1950	9648	61030	49571	2509	773	123531	96046	3636
1951	3636	6788	38252	23587	1011	73274	64647	3255
1952	3255	3305	2596	19180	6451	34787	31830	62037
1953	62037	2926	2244	513	3207	70927	28092	125313
1954	125313	46631	1533	756	543	174776	57878	50070
1955	50070	84374	34066	766	1044	170320	104728	81795
1956	81795	43779	42693	16696	366	185329	100035	21196

1957	21196	47760	23617	15188	6815	114576	84594	24184
1958	24184	11879	14738	5962	2778	59541	39377	88151
1959	88151	29150	7930	3830	2047	131108	53892	58799
1960	58799	58641	19054	4481	1800	142775	79608	126860
1961	126860	67164	29087	5352	892	229355	96783	86791
1962	86791	130399	45235	10976	1453	274854	159173	13744
1963	13744	61556	90361	22556	4122	192339	155462	8160
1964	8160	13588	30741	55323	9503	117315	104241	2044
1965	2044	3218	4129	11932	19188	40511	38057	4021
1966	4021	2177	2375	1719	10275	20567	17634	575
1967	575	1122	675	626	1727	4725	4111	1141
1968	1141	339	743	232	820	3275	2569	4075
1969	4075	194	140	210	280			

* Spawning biomass was calculated with the percentage of age 1 spawners as in Figure 14: 77%, 88%, and 100% of ages 2, 3, and 4 were considered mature. (Estimates before 1939 and after 1967 are unreliable).

third and most interesting hypothesis is that the increase in variance is the result of decreased spawning biomass.

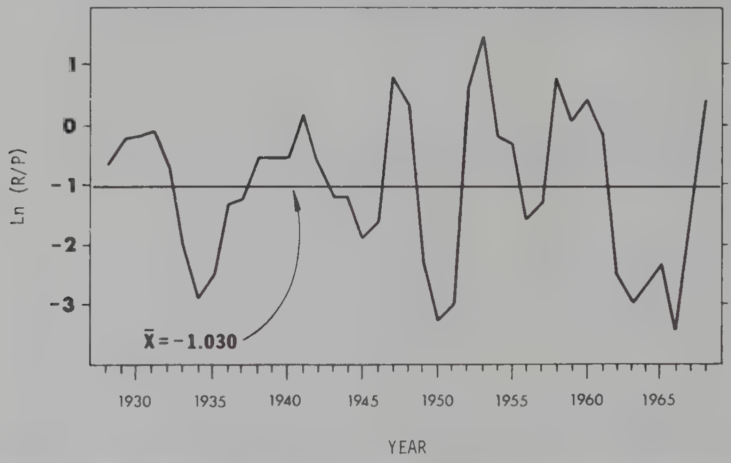

FIGURE 9. Time series of the natural log of the observed recruit biomass per spawning biomass.

Overall spawning success is an average of all the results from individual spawning events in a given season. These events could be considered to be samples drawn from the total spawning environment, which extends through space and time. The true average spawning environment certainly changes from year to year, but presumably fluctuates about a mean set of conditions which reflect the long-term average. If we assume randomness of spawning behavior with respect to subsequent conditions affecting larval survival, the hypothesis can be viewed as a basic statistical sampling problem. By treating mean biomass as an index of sample size, we can use the property that the standard error of the mean varies inversely with the square root of the sample size as an approximation. Thus, on the basis of population size, we would expect a relative increase in standard error of 1.64 (i.e. $\sqrt{286/106}$), whereas the actual increase was 1.89. The additional increase, if it is other than random error, could result from several causes. The temporal extent of spawning is largely dependent on the age structure of the population, and the mean age of the

TABLE 15. Comparison of Spawning Success for Two Periods of the Pacific Mackerel Fishery.

Period	*1928–1945*	*1946–1968*
Number of years	18	23
Mean index of spawning success	−0.984	−1.067
Standard error*	0.861	1.628
Mean spawning biomass (million pounds)	286	106
Mean age of spawning biomass at beginning of season	3.21	2.65

* F statistic = 3.575; $P(F_{22,17}\ 3.12) = 0.01$

spawning biomass was lower for the latter period (Table 15). Also, the spawning environment is very contagiously distributed in space and time (Lasker, 1975), suggesting that small sample sizes would be highly variable. If the third hypothesis is correct, maintenance of a larger spawning biomass might have helped the stock survive the poor spawning successes of the 1960's. Presumably, the recruitment failures would have been somewhat more moderate, and the larger surviving biomass would have aided recovery when better spawning successes returned in the late 1960's and 1970's.

RECRUITMENT MODELS

METHODS

The statistical procedures used in this report included extensive use of correlation and regression techniques. The Statistical Interactive Programming System (SIPS) developed and maintained by the Oregon State University Statistics Department (Guthrie, Avery, and Avery 1974) was used almost exclusively for the early analyses. Forward stepwise multiple regression as described by Draper and Smith (1966) was used for analysis including environmental variables. Later analyses included non-linerar regressions. These analyses used the Biomedical Computer Program BMDP3R (Dixon 1975). Several of the BMDP3R subroutines were altered for use on a CDC 6500. The program was altered by the addition of the FORTRAN statements necessary to fit the functions used in the various recruitment models.

Density-dependent recruitment functions

Spawner-recruit functions of several types were fitted to the estimates of recruit biomass (i.e., at age 1) and spawning biomass. The three principal density-dependent functions used were those used by Ricker (1975: 282), Beverton and Holt (1957: 49), and Cushing (1971). These three functions are shown in Figure 10. The major difference in the three functions is the amount of prerecruitment mortality associated with increasing population density (i.e., compensatory mortality). The Ricker function predicts that recruitment increases to a maximum at some moderate spawning biomass level and then decreases to low recruitment at a high

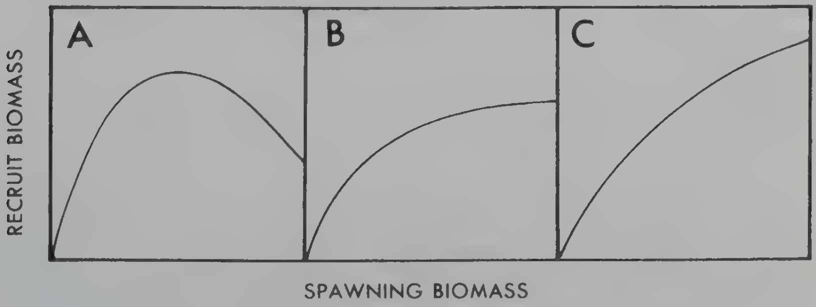

FIGURE 10. Density-dependent spawner-recruit models; A. Ricker, B. Beverton and Holt, C. Cushing

spawning biomass levels. The Beverton and Holt function predicts that recruitment increases to an asymptote as spawning biomass increases. The Cushing function predicts that recruitment continues to increase without bounds with increasing spawning biomass, however at a diminishing rate.

Clark (1974) has suggested that increased mortality may occur at low biomass levels in pelagic schooling fishes (i.e., depensatory mortality). This increase in mortality rate at low biomass levels would be caused by a decrease in the average school size, which would result in a reduction in the survival value of schooling. Two spawner-recruit functions were used to determine if Clark's hypothesis could be used to improve the spawner-recruit relationship in a stock that had suffered recruitment failure. These two spawner-recruit functions were made by including a depensatory term in the Ricker and Cushing spawner-recruit functions.

The five spawner-recruit functions were fitted with linear regressions, with log transformed variables, and nonlinear regressions. The equations for the five models and the regression variables used to fit the linear regressions are listed in Table 16. The r^2 and F values for the transformed linear regressions were calculated by the SIPS program. These values for the linear and curvilinear models were calculated by a short FORTRAN program which calculates the total sum of squares, corrected for the mean, and the residual sum of squares for the regression models.

TABLE 16. Regression Variables for Spawner-Recruit Functions

		Linear regression variables	
Name	*Function*	*Dependent*	*Independent*
Ricker	$R = b_1Pe^{-b_2P}$	$\ln(R/P)$	P
Cushing	$R = b_1 P^{b_2}$	$\ln(R)$	$\ln(P)$
Beverton and Holt	$R = (P/[b_1 + b_2/P])$	P/R	P
Clark-Ricker	$R = b_1Pe^{-b_2P}e^{-b_3/P}$	$\ln(R/P)$	$P, 1/P$
Clark-Cushing	$R = b_1 P^{b_2} e^{-b_3/P}$	$\ln(R)$	$\ln(P), 1/P$

Where

R = Recruit biomass

P = Parent biomass

b_1 = Density independent coefficient

b_2 = Compensatory, density dependent coefficient

b_3 = Depensatory, density dependent coefficient

Environmental variables

The environmental data used in this study are available primarily as monthly means. Annual environmental factors, such as Bakun's (1973) upwelling indices or sea surface temperature at Scripps pier, therefore consisted of 12 individual variables. These variables are not completely independent. For example sea surface temperatures from adjacent months are obviously highly correlated. In fact seasonal patterns, in the association between the monthly means and recruitment, occurred in most of the environmental factors. The lack of independence between the monthly means was not a necessary prerequisite in the development of recruitment models. The models were developed with stepwise regression, which does not require that all potential variables be completely independent.

The major spawning season for Pacific mackerel is May-July. The monthly means discussed above may cover too small a portion of the spawning season to test the associations between environmental conditions and recruitment. To assess the associations between longer term environmental conditions and recruitment, several 3-month combinations were made. The first combination was the mean value for the three main spawning months (May-July). On the hypothesis that conditions immediately prior to spawning should influence spawning, the second combination was the mean value for April-June. As previously noted there is a marked seasonal difference in the peak of maturity in Pacific mackerel of different ages. It was thought therefore that the age structure of the population would influence the recruitment response to environmental variables. For example a spawning population consisting primarily of age 1 fish, which have a maturity peak in July, would not be able to take advantage of favorable environmental conditions occurring in May. Therefore, linear combinations of the environmental variables from May-July and April-June were made. These linear combinations were prorated by Pacific mackerel age composition of an individual year. For example, if the age composition of the spawning biomass in a given year was 50% ages 3+, 20% age 2, and 30% age 1, the prorated variable was 50% of the May value, 20% of the June value, and 30% of the July variable. The same procedure was used for the prorated April-June variables.

The large number of environmental variables analyzed for this study necessitated that some pre-analysis be carried out before multiple regression models were developed. The pre-analysis was accomplished by calculating the correlation coefficient for the relationship between each environmental variable and recruitment. Three different correlations were made for each environmental variable. These three were the correlations with the recruit biomass (i.e., at age 1), the natural log of recruit biomass, and the natural log of the recruit biomass divided by the spawning biomass. Hereafter the above three will be referred to as R, ln(R), and ln(R/P).

The choice of environmental variables to include as potential variables in recruitment functions for Pacific mackerel was largely dependent upon available long-term data. Unfortunately such data were not available on plankton populations. Data sources were limited therefore to physical oceanographic and meteorological data.

Environmental data analyzed can be grouped into three general categories based on the period of coverage. Category one includes land-based meteorological, sea level and sea surface temperature data. The period covered by these data includes the entire period of the data base of the population estimates (1928-1968). Data analyzed included monthly mean atmospheric pressure at San Diego, mean sea level difference between San Francisco and Hilo, Hawaii (Saur 1972), monthly mean sea surface temperature at Scripps pier, and the monthly mean sea level at La Jolla.

Sea level data were included as a potentially important variable because of the relationship between geostrophic flow and coastal sea levels. Reid and Mantyla (1976) have shown a close relationship between seasonal geostrophic flow and sea level elevations at La Jolla, California.

The second category included ship observation data. These data are available as monthly means by 5 degree blocks (i.e., Marsden Square quadrants). The data base starts in 1931. Data analyzed included wind speed, sea surface temperature, and cloud cover for Marsden Square quadrants 120 (2) and 84 (3) (Figure 11). All of the data for Marsden Squares and for sea level at La Jolla was provided by the Pacific Environ-

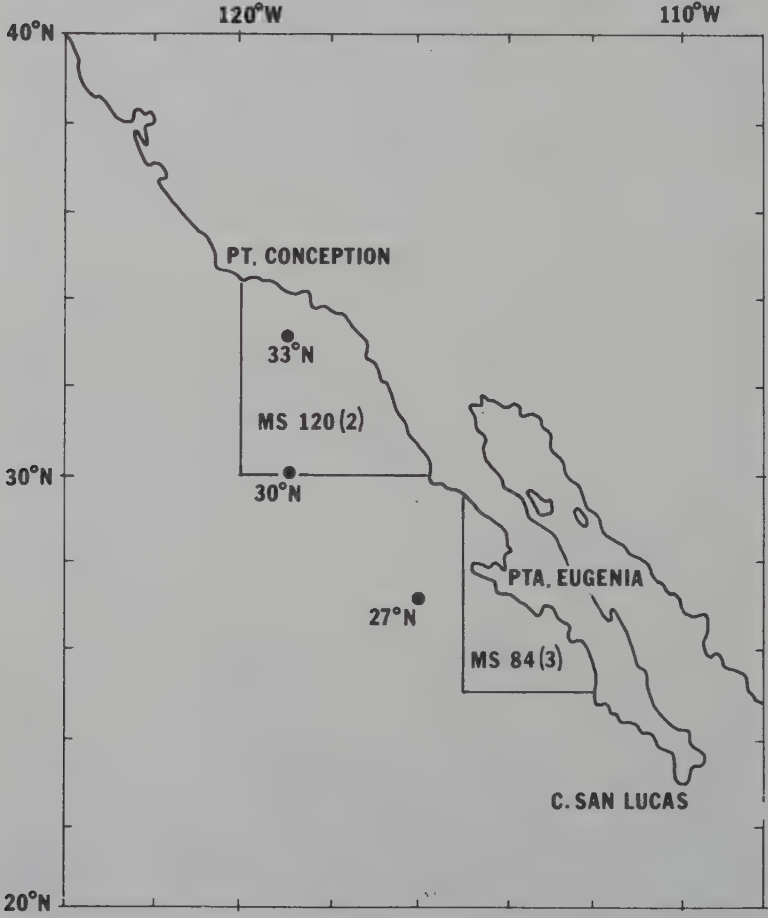

FIGURE 11. Marsden Square quadrants 120(2) and 84(3), and upwelling index locations

mental Group of the National Marine Fisheries Service. Data on wind speed were included as it would be expected to be related to upwelling. Cloud cover could be important because it might be used as an index of insolation and it could also be related to upwelling.

The third category is composed of data from a series of mass transport calculations. The data were provided by Bakun (pers. comm.) and his calculations were made with the procedures described by Fofonoff (1960). Data analyzed included meridional total transport, meridional Ekman transport, divergence of Ekman transport [Bakun's (pers. comm.) offshore divergence indices], and Bakun's (1973) coastal upwelling indices (i.e., Ekman transport perpendicular to the coast). The transport calculations were based on a 3° grid of monthly mean atmospheric pressure which was interpolated from pressure fields prepared by Fleet Numerical Weather Central, U.S. Navy. The data base starts in 1946. Analysis of the transport data included the calculations at three locations: 27°N, 30°N and 33°N (Figure 11). Nelson et al. (1976) have shown that Ekman transport, calculated by Bakun's (1973) methods, accounts for 84 percent of the variation from a Ricker spawner-recruit curve in Atlantic menhaden.

The four sets of transport data are actually indices of two processes. Bakun's (1973) upwelling indices and meridional Ekman transport are different angular components of wind-driven transport. The units of measure in these components are metric tons per second per 100 m. width. The second mechanism is wind stress curl, which is a measure of the rate of change of wind driven transport with respect to space. Sverdrup (1947) has shown that meridional total transport is proportional to wind stress curl. The divergence of Ekman transport, which is proportional to total meridional transport minus meridional Ekman transport, is dominated by total transport and is therefore essentially the same as wind stress curl. Units of the two measures of wind stress curl are given in terms of vertical velocity (millimeters per day, positive upwards) through the bottom of the Ekman layer.

Environmental-dependent recruitment functions

Recruitment models incorporating both population and environmental variables were developed with stepwise multiple regression. The on-line statistical system used for stepwise multiple regressions (SIPS) is limited to 50 variables, so it was necessary to reduce the number of potential independent variables. The independent variables used were the previously discussed linear combinations of the spawning months and all other variables with a significant correlation (95% level) with the dependent variable.

In Pacific mackerel the environmental variables were more strongly correlated with recruitment than were the population variables. It was felt that the size of the parent stock must have underlying effects on recruitment as suggested by Clark (Clark and Marr 1955). The fact that recruitment is heavily dependent upon environmental factors does not negate the effects of parent stock size; it merely masks the effects. Therefore the multiple regression models developed included population variables. The models were developed by adding the population variable to the regression model before the stepwise process was started (i.e., forcing in the population variable before any environmental variables were allowed to enter the regression). This had the effect of adding environmental variables that best describe recruitment given the fact that a population variable is included in the model. However, this is not to say that the multiple regression models describe variation from the density-dependent Ricker or Cushing models.

DENSITY-DEPENDENT RECRUITMENT FUNCTIONS

Spawner-recruit functions were calculated with both linear and nonlinear regression procedures. The linear regression models were fitted with log transformed variables and will hereafter be referred to as transformed models. The exponentiated versions of the transformed models will be referred to as the linear models. Transformed models for the period of 1928–1968 were significant at the 1% level for the Cushing function but the Ricker and Beverton and Holt functions were not significant even at the 5% level (Table 17). None of the linear models is significant at the 5% level. The linear Cushing and Beverton and Holt models had a larger sum of squares than the total sum of squares corrected for the mean. This implies that the linear Cushing and Beverton and Holt models provide significantly worse estimates of recruitment than does mean recruitment.

The nonlinear (BMDP3R) Ricker and Cushing functions are both significant at the 99% level (Table 17). The addition of a depensatory term to the Ricker and Cushing functions only slightly increased the coefficients of determination (r^2); the Clark-Ricker function was significant at the 5% level (Table 17). The Clark-Ricker function converged to a positive coefficient and therefore this model contains two compensatory terms rather than a compensatory term and a depensatory term. The fact that the addition of depensatory terms did not improve the fits of the spawner-recruit functions does not necessarily imply that a depensatory recruitment factor does not exist in Pacific mackerel. The large observed variation in recruitment at low spawning biomass levels would have hindered detection of a depensatory factor and it is possible that depensation would not occur until the spawning biomass reached extremely low levels.

The three Ricker models (Table 17) have very low density-independent coefficients. This suggests that the limiting equilibrium rate of exploitation will be quite low in comparison to other fisheries (Ricker 1975:286). The poor statistical fit of the Ricker model is apparent in the large variation in ln(R/P) that occurred when the spawning biomass was less than 200 million pounds (Figure 12).

Fitted curves for the linear and nonlinear Ricker and Cushing functions are shown in Figure 13. The curves for the linear functions show considerable similarity in form at spawning biomass levels below 350 million pounds. The nonlinear, BMDP3R, Ricker and Cushing curves also show considerable similarity. It appears that at least for low and moderate spawning biomass levels the way the functions are fitted is more important than which function is used.

TABLE 17. Density-dependent Spawner-recruit Functions

Name	*Function*	R^2	*F*	*DF*
Cushing transformed	$\ln(R) = 2.0948 + 0.72888 \ln(P)$	0.297	16.49**	1,39
Cushing linear	$R = 8.1238\ P^{0.72888}$	–	–	1,39
Cushing nonlinear	$R = 1069.9\ P^{0.36187}$	0.166	7.78**	1,39
Beverton and Holt transformed	$P/R = 6.1961 + 0.0000030821\ P$	0.002	0.09	1,39
Beverton and Holt linear	$R = P/(6.1961 + 0.0000030821\ P)$	–	–	1,39
Ricker transformed	$\ln(R/P) = -0.67752 - 0.00000214\ P$	0.068	2.85	1,39
Ricker linear	$R = 0.50787\ Pe^{-0.00000214P}$	0.057	2.31	1,39
Ricker nonlinear	$R = 0.88093\ Pe^{-0.00000253P}$	0.236	12.06**	1,39
Clark-Cushing nonlinear	$R = 2435.4\ P^{0.29910}\ e^{-7524.3/P}$	0.170	4.39*	2,38
Clark-Ricker nonlinear	$R = 0.85112\ Pe^{-0.00000242P}\ e^{3501/P}$	0.237	5.90**	2,38

R = Recruit biomass in thousands of pounds
P = Parent biomass in thousands of pounds
* = Significant at 5% level
** = Significant at the 1% level

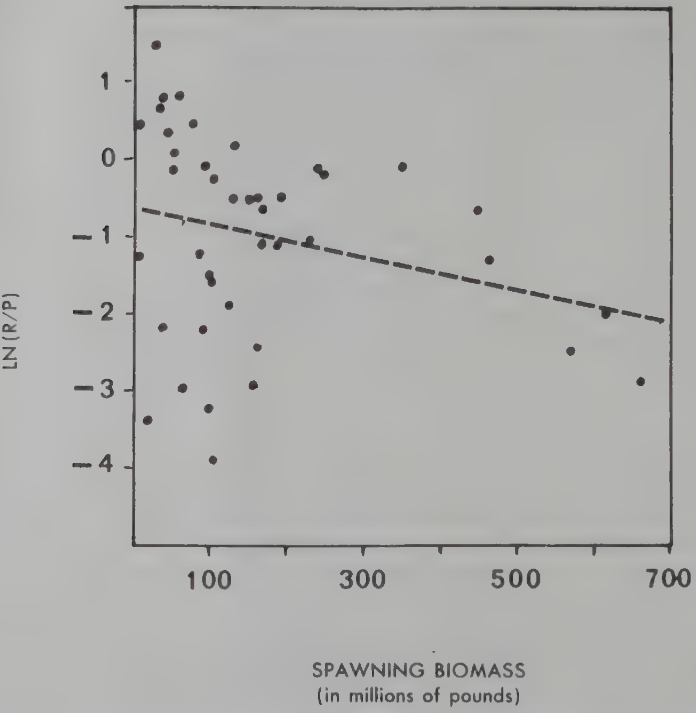

FIGURE 12. Natural logarithms and regression line of recruit biomass per spawning biomass plotted against spawning biomass

The Cushing and Ricker models above were transferred to spawner resultant-spawner models to show equilibrium points (Figure 14). This transfer was calculated by multiplying the calculated recruitment by a factor that determines the spawning biomass of a cohort that would occur when there was no fishing mortality. This factor (3.845) was calculated by the ISOE program (Appendix I). The resulting spawning biomass per unit weight of recruits calculated with this program assumed a constant (0.26) proportion of maturity of age 1 fish. With the assumption of density-dependent maturity of age 1 fish the spawn resultant spawner relationship would be somewhat more arched than shown in Figure 12 and the equilibrium points would be at a lower spawning biomass.

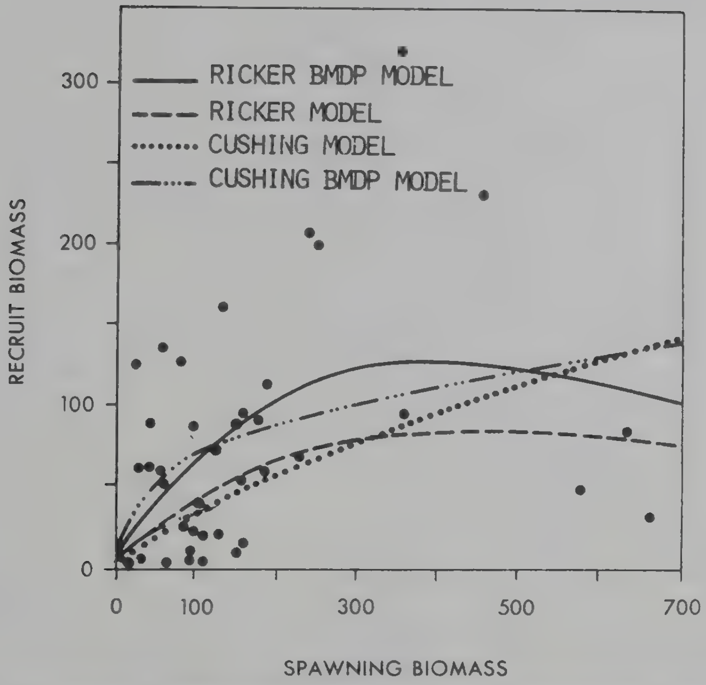

FIGURE 13. Ricker and Cushing spawner-recruit models fitted to Pacific mackerel population data. (Values in millions of lbs.).

ASSOCIATIONS BETWEEN RECRUITMENT AND ENVIRONMENTAL FACTORS

Sea surface temperature

Off southern California, warm sea surface temperature during the spawning season was found to be associated with good recruitment in Pacific mackerel. This pattern was seen in the Marsden Square quadrant off southern California, 120(2), and at Scripps pier (Figure 15). The sea surface temperature off Baja California, Marsden Square quadrant 84(3), did not show this relationship (Figure 15). After the correlations were calculated it was found that the 84(3) quadrant contained observations from the Gulf of California and this undoubtedly biased the data from this quadrant.

The generally expected relationship between sea surface temperature (SST) and the number of recruits per spawner is a dome-shaped curve (Ricker 1975:276). The number of recruits per spawner should rise to a maximum at some optimum temperature and then decline to lower levels

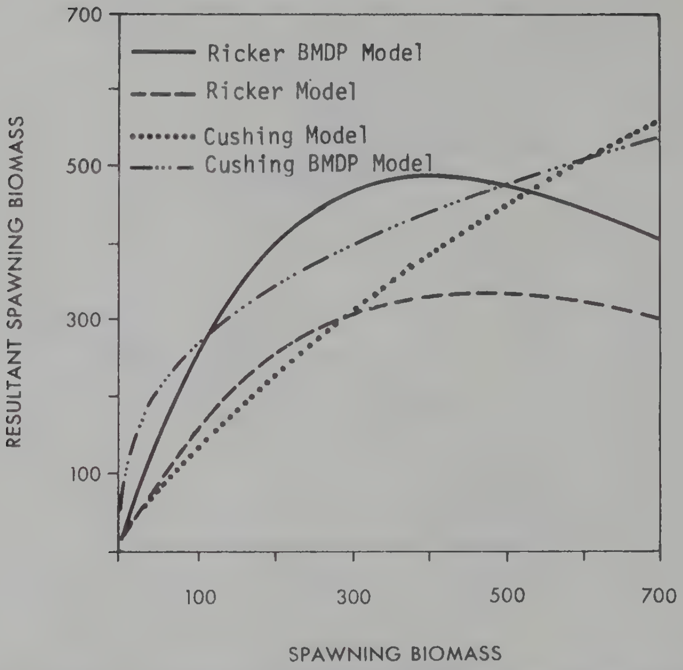

FIGURE 14. Ricker and Cushing spawner resultant-spawner models (values in millions of lbs)

as temperature continues to increase. The above pattern would be expected to occur in the center of the species' geographical range. The California stock of Pacific mackerel is on the northern, cold-water edge of the range of the species. The fact that upwelling is most intensive during the spawning season of Pacific mackerel also contributes to depressing SST. Therefore the dome-shaped relationship between SST and the number of recruits per spawner should not be expected to hold for the California stock of Pacific mackerel because the SST does not get high enough to depress recruitment. To approximate this relationship a quadratic multiple regression of ln (R/P) vs. T and T^2 was calculated (where T = prorated April–June sea surface temperature (C°) in Marsden Square 120(2)). The first order value of temperature is the first variable to enter, with an r^2 of 0.2611 (F = 12.72** with 36 df). The entering of the second order term is not significant and the r^2 is only increased to 0.2613. The hypothesis that the relationship between ln(R/P) and SST is quadratic must therefore be rejected for the range of SST observed in Marsden Square 120(2). The first order regression equation is significant at the 99% level.

$$\ln(R/P) = -13.527 + .78815\ T^{**}$$

This model suggests that warm surface waters are positively associated with good spawning success; however, the relationship shown should only

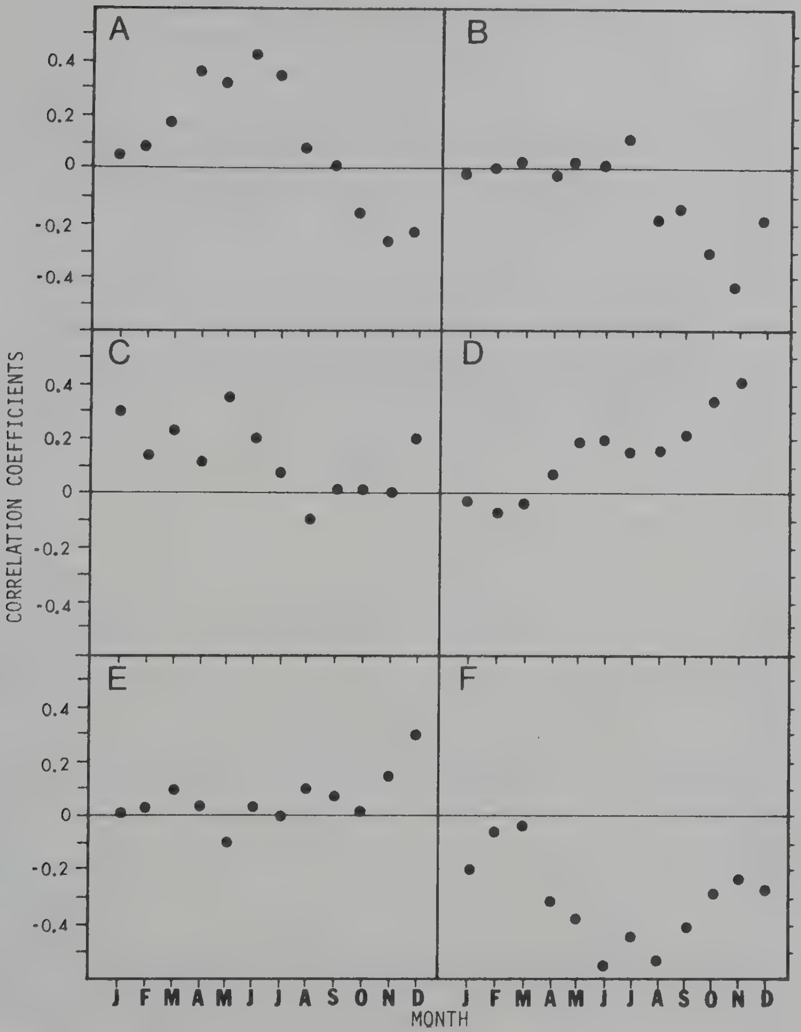

FIGURE 15. Correlations of ln(R) with monthly environmental factors; A. SST in Marsden square 120(2), B. SST in Marsden square 84(3), C. SST at Scripps Pier, D. Sea level differences from Saur (1973), E. Sea level barometric pressure at San Diego, F. Sea level at La Jolla

be considered valid with Marsden Square 120(2) sea surface temperatures between 14° and 17.5°C. It should be noted that only 26% of the variation in ln(R/P) is explained by these data.

Sea level and atmospheric pressure

Monthly mean sea level at La Jolla, corrected for atmospheric pressure, and Saur's (1972) sea level differences between San Francisco and Hilo, Hawaii show different correlation patterns with recruitment. There is a statistically significant negative correlation between recruitment in Pacific mackerel and the sea level at La Jolla for the entire April–September spawning season, (Figure 15). Saur's sea level differences do not show a statistically significant correlation with recruitment during the spawning season but do show positive correlation during the late fall (Figure 15). Monthly means of barometric pressure at San Diego show little correlation with ln(R), (Figure 15).

Wind speed and cloud cover

Wind speeds in both Marsden Squares show a constant negative correlation with ln(R), (Figure 16). Cloud cover appears to have little association with ln(R) and with the exception of one month the correlations are not significant at the 95% level (Figure 16).

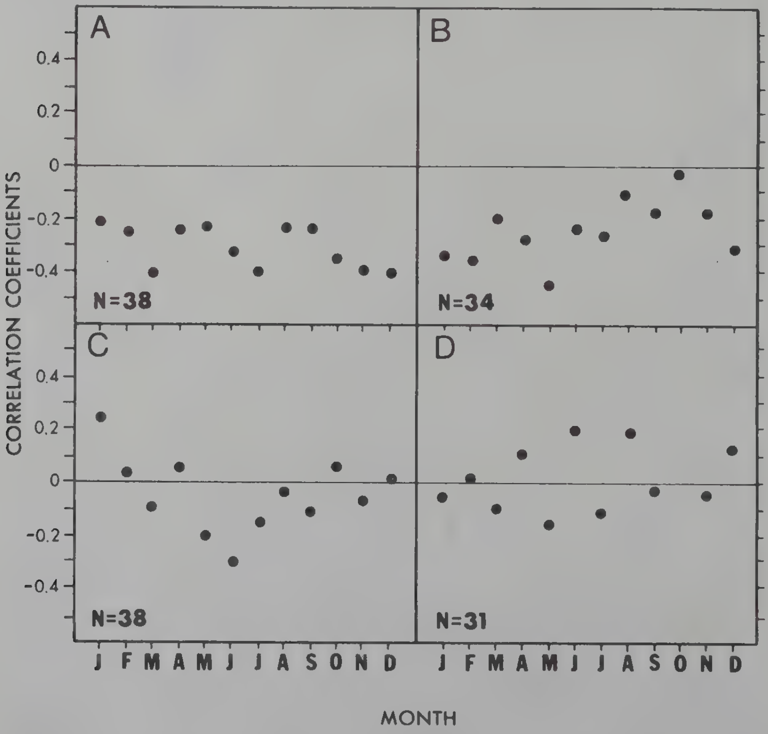

FIGURE 16. Correlations of ln(R) with monthly environmental factors; A. Wind speed in Marsden square 120(2), B. Wind speed in Marsden square 84(3), C. Cloud cover in Marsden square 120(2), D. Cloud cover in Marsden square 84(3).

Ekman and total transport

Associations between ln(R) and transport data tended to show higher correlations than ln(R) and Marsden Square or shore-based data sets. Data from 30°N tended to be correlated considerably better with ln(R) than data from 33°N and slightly better than data from 27°N. This is consistent with the observed center of larval distribution (Figure 3).

Bakun's (1973) upwelling indices at 30°N, positive offshore, show spring and fall peaks in association with ln(R) (Figure 17). Meridional Ekman transport at 30°N shows to a lesser extent the same spring and fall peaks as Bakun's upwelling indices. Values for meridional Ekman transport were calculated with negative values southward, which accounts for the difference in the sign of the correlation coefficients between the upwelling indices and meridional Ekman transport. There is a positive correlation between ln(R) and the upwelling indices. This relationship is conceptually satisfying in that increased plankton production resulting from upwell-

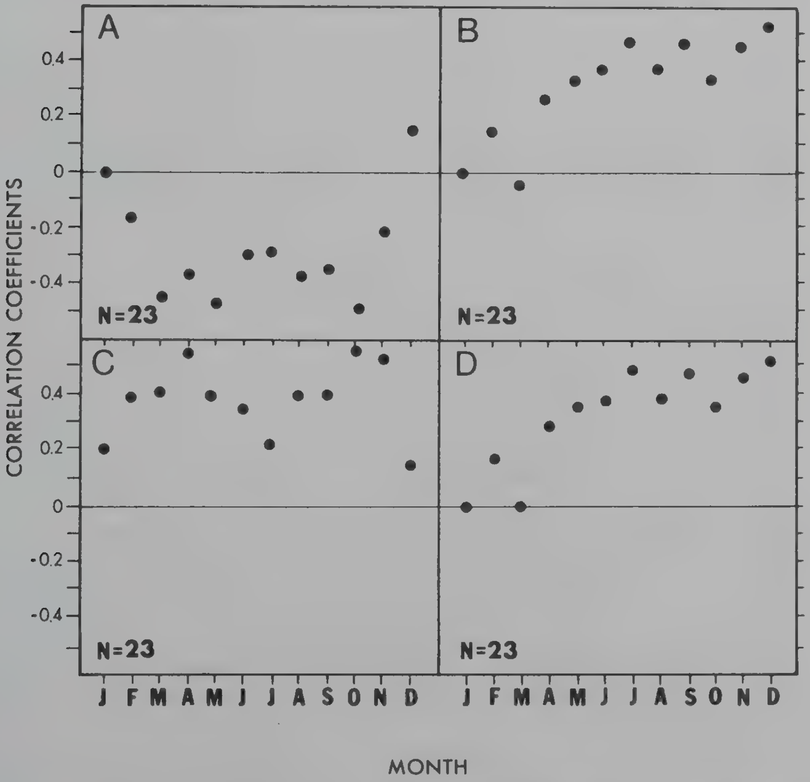

FIGURE 17. Correlations of ln(R) with monthly environmental factors; A. Meridional Ekman transport at 30°N; B. Meridional total transport at 30°N; C. Bakun's (1973) upwelling indices at 30°N; D. Divergence of Ekman transport at 30°N.

ing should be beneficial to larval fishes. It is also noteworthy that the peak of spawning in Pacific mackerel is the same as the peak of upwelling off central Baja California (i.e., May–June).

Meridional total transport shows significant, positive correlation with ln(R) during the end and after the spawning season (Figure 17). The divergence of Ekman transport shows essentially the same monthly correlation pattern as total meridional transport. Total meridional transport and the divergence of Ekman transport at 30°N (wind stress curl) are atypical for the California Current region in that the values are negative. Bakun and Nelson (in press) have shown that negative wind stress curl (convergence), which is characteristic of the offshore region, extends toward the coast in the region just north of Punta Eugenia. They point out that the patterns of negative and positive wind stress curl suggest separate cyclonic gyres in the regions of positive wind stress curl off the Los Angeles Bight and south of Punta Eugenia (Figure 18). They also note that ship-drift data in the region of negative wind stress curl tend to confirm this hypothesis in that a poleward component is lacking during the fall when the relaxation of upwelling would favor surfacing of a coastal counter current.

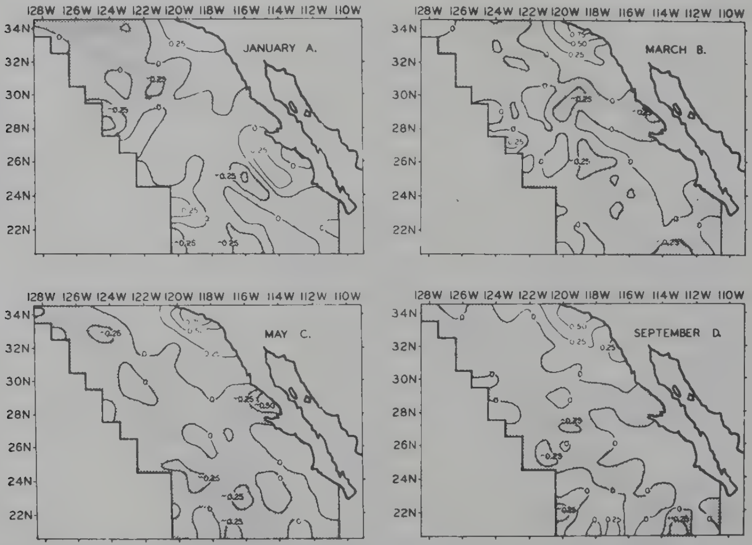

FIGURE 18. Wind stress curl patterns off southern California and Baja California (Bakun and Nelson In Press)

Linear combinations of spawning months

Several combinations and prorations of the spawning months resulted in larger correlation with recruitment (ln(R)) than did the individual months (Table 18). Some of this increased correlation may have been fortuitous. However, it is conceptually satisfying that environmental conditions over the entire spawning season are better correlated with recruitment than conditions occurring in any one month. We feel that it is noteworthy that the environmental variable found to have the highest correlation with recruitment is one with very strong biological implications. This variable, April–June upwelling indices at 30°N prorated by the age composition of the spawning biomass, had a correlation coefficient of 0.713 with ln(R). Over 50 percent of the variation in ln(R) is explained by this variable. The high correlation with this variable suggests that recruitment is increased if there is upwelling just prior to and during the early part of the spawning season. It also implies that changes in age structure, and therefore time of peak spawning, can alter the response to a given upwelling pattern. It should also be noted that prorating the May–July upwelling indices by the age composition reduced the correlation with ln(R) to 0.319. The implications are that upwelling a month prior to peak spawning results in greatly increased reproductive success and that upwelling during peak spawning does not significantly increase reproductive success. The above is an agreement with field observations for the northern anchovy which suggest that storms and strong upwelling disperse chlorophyll maximum layers that provide forage necessary for survival of first-feeding anchovy larvae (Lasker 1975, 1978).

TABLE 18. Correlation Coefficients of Linear Combinations of Monthly Values of Environmental Variables with ln(R)

Variable	*N*	*May–July mean*	*Prorated*[1] *May–July*	*April–June mean*	*Prorated*[1] *April–June*
SPIER	41	.270	.416**	.276	.255
BARP	41	.030	−.165	−.007	−.059
SSTC	38	.434**	.432**	.432*	.392*
WINDC	38	−.364*	−.380*	−.289	−.306
SLLJ	41	−.542**	−.391**	−.514**	−.392**
SLEV	41	−.509**	−.348*	−.509**	−.366*
UP	23	.458**	.319	.575**	.713**
ODI	23	.528**	.610**	.486*	.584**

SPIER —Sea surface temperature at La Jolla
BARP —Barometric pressure at San Diego
SSTC —Sea surface temperature, Marsden Square quadrant 120(2)
WINDC —Wind speed, Marsden Square quadrant 120(2)
SLLJ —Uncorrected sea level height at La Jolla
SLEV —Sea level height at La Jolla corrected for atmospheric pressure
UP3 —Bakun's (1973) upwelling index at 30°N
ODI3 —Bakun's (pers. comm.) offshore divergence index at 30°N (divergence of Ekman transport).
* —Significant at 5% level
** —Significant at the 1% level
1 —Variables were prorated as described on page 27

ENVIRONMENTAL-DEPENDENT RECRUITMENT FUNCTIONS

Recruitment functions incorporating both density-dependent and environmental-dependent factors were developed with forward stepwise multiple regression procedures. This limited the possible recruitment models to functions that are linear or functions that can be transformed to linear functions. It was decided that the use of exponential environmental terms was the most promising as both the Ricker and Cushing spawner-recruit functions can be fitted with linear regression of log transformed terms. This approach has been recommended by Ricker (1975), who suggests that the expected effects of the physical environment are multiplicative rather than additive and therefore logarithms should be used in multiple regressions. Log transformed functions are fitted to the geometric mean rather than the arithmetic mean. When these functions are transformed back to the original form they are biased towards low values. To avoid this bias the parameters of the spawner-recruit functions developed with stepwise multiple regression were computed by regressing the functions with the BMDP3R nonlinear regression program. This program requires a FORTRAN subroutine, which principally consists of the individual functions and the partial derivatives of the parameters of the functions. The subroutine used for all nonlinear regressions is listed in Appendix III.

The stepwise multiple regression models were fitted, as previously described, with the density term assigned as a forced variable in the forward stepwise process. The density terms were ln(P) for the Cushing function and P for the Ricker function. Entering environmental terms were accepted if their entering F values were significant at the 95% level. The exception to this is that the number of variables accepted was limited by the number of observations in each case. Draper and Smith (1966:167) suggest that the fitted model should not have more than one variable for every 5 to 10 observations.

Models were developed over three different time periods. Models developed for the first time period (1931–1968) included the Ricker and Cushing based models fitted with the Marsden Square and shore-based data sets. A Ricker based model was developed for the same data set for the reduced period of 1931–1960. This model was used to determine if the population decline of the mid-1960's would be predicted with a model that was fitted to data that did not include this population decline. The third set of models included the Ricker and Cushing based models fitted with all environmental data sets (1946–1968).

It was decided to limit the multiple regression models fitted to the 1931–1968 data sets to four independent variables due to the number of observations (38). The four variables were the density term and three environmental terms. The model fitted to the 1931–1960 data sets was not fitted by stepwise multiple regression. This multiple regression model was used for comparative purposes and it was decided that it would include only the density and environmental variables that were in the comparable 1931–1968 model.

The models developed from the 1946–1968 data sets were limited to three independent variables, the density term and two environmental terms due to the smaller number of observations (23). The stepwise multiple regression models based on the Ricker and Cushing functions did not always select the same environmental variables. For example in the 1931–1968 models the Cushing-based model selected the May–July mean sea surface temperature and the Ricker-based model selected the April–June prorated sea surface temperature (SSTC, Table 2). The two variables have very similar correlation coefficients with ln(R) and r^2 values were essentially the same in both the Cushing and Ricker based models. Due to the similarity of r^2 values it was decided to incorporate the identical environmental variables in the Cushing and Ricker based models for simplicity.

To avoid confusion in later analysis with the environmental-dependent recruitment functions, the functions will hereafter be referred to by the following names: 1) The functions fitted to the 1931–1968 data sets will be called the Ricker sea level model and the Cushing sea level model. The name refers to the first environmental variable to enter the stepwise regressions; 2) The reduced Ricker sea level model will refer to the function fitted to the reduced 1931–1960 data set; 3) Functions fitted to the 1946–1968 data sets will be called the Ricker transport model and the Cushing transport model.

The five environmental-dependent spawner-recruit functions used in the report are listed in Table 19. The environmental variables that provide the best description of recruitment in Pacific mackerel from 1931–1968 are May–July mean sea level at La Jolla; prorated mean May, June, and July barometric pressure at San Diego; and mean April–June sea surface temperature in Marsden Square quadrant 120(2). The Ricker and Cushing sea level models had very similar r^2 values, 0.587 and 0.597, and the F statistics for these models were approximately three times as large as the critical F value at the 99% significance level (Table 19). The reduced Ricker sea level model has an r^2 of 0.517. Its F statistic was considerably smaller than the other two sea level models but was still significant at the 99% level.

The Ricker and Cushing transport models include two environmental variables. Both of these variables describe surface transport. The first variable is the April, May and June offshore divergence indices at 30°N prorated by the age composition of the spawning biomass. The Ricker transport model has an r^2 of 0.756 and a F statistic of 19.59 (Table 19). The corresponding statistics for the Cushing transport model are 0.676 and 13.31. The critical F statistic at the 99% level of significance is 5.01.

The predicted recruitment with the Ricker and Cushing sea level models and the observed recruitment are shown in Figure 19A. The same data for the transport models are shown in Figure 19B. The sea level model provides a reasonable description of the general periodicity of recruitment but individual years are not well estimated. The transport model shows a close agreement with the observed recruitment. The only year that is markedly different in observed and predicted recruitment is 1961.

FACTORS AFFECTING RECRUITMENT

The spawning biomass of Pacific mackerel undoubtedly establishes the limits on the possible size of an individual year class. Within these limits recruitment is heavily dependent upon physical environmental condi-

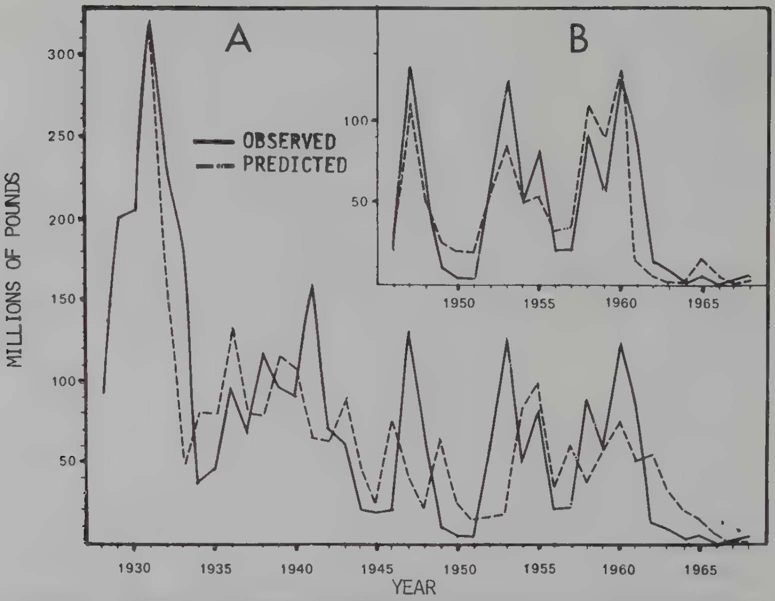

FIGURE 19. Observed and predicted recruitment of Pacific mackerel A. Ricker sea level model, B. Ricker transport model.

TABLE 19. Environmental-dependent Spawner-recruit Functions

Function name	*Period covered*	*R²*	*F*	*DF*
Ricker sea level $R = 51608Pe^{-0.00000353\,P}e^{-2.5004\,SLEV}$ $e^{-0.25594\,BARP}e^{0.53309\,SSTC}$	1931–1968	0.587	11.72 **	4,33
Cushing sea level $R = 100850000P^{0.095703}e^{-2.7680\,SLEV}$ $e^{-0.09858\,BARP}e^{0.65528\,SSTC}$	1931–1968	0.597	12.22 **	4,33
Reduced Ricker sea level $R = 4214.2Pe^{-0.00000351\,P}e^{-2.1837\,SLEV}$ $e^{-0.19759\,BARP}e^{0.51148\,SSTC}$	1931–1960	0.517	6.68 **	4,25
Ricker transport $R = 0.97815Pe^{-0.0000377\,P}e^{0.020787\,UP}$ $e^{0.0039065\,ODI}$	1946–1968	0.756	19.59 **	3,19
Cushing transport $R = 43577000P^{-0.84881}e^{0.02350\,UP}$ $e^{0.00469\,ODI}$	1946–1968	0.676	13.31 **	3,19

R — Recruit biomass at age 1 in thousands of pounds
P — Parent spawning biomass in thousands of pounds
SLEV— Mean May-July sea level at La Jolla, California in feet (corrected for atmospheric pressure)
BARP— Sea level barometric pressure at San Diego May, June and July mean pressure prorated by the age composition of the spawning biomass (in millibars minus 1000 millibars)
SSTC— Mean April-June sea surface temperature in Marsden square quadrant 120(2), (in degrees celsius)
UP — Bakun's upwelling index at 30°N. April, May and June indices prorated by the spawning biomass (in M³ per second across 100m width)
ODI — Bakun's (pers. comm.) offshore divergence index at 30°N (Divergence of Ekman transport). April, May, June indices prorated by the spawning biomass (in mm per day positive upwards)
** — Significant at the 1% level

tions. Interrelations with other species also play a role in determining recruitment (Hunter 1976). However, the direct relationship between the populations of other species and recruitment in Pacific mackerel is difficult to demonstrate with available data.

Over the period of 1928 to 1968 the estimated recruit biomass varied from 0.58 to 321 million pounds (260 to 145,603 metric tons). Recruitment success therefore varied by a factor of 560. Density-dependent recruitment models account for a maximum of about 24 percent of the variation in recruitment. Recruitment models incorporating both density-dependent terms and environmental terms account for about 60 percent of the variation in recruitment from 1931–1968 and about 75 percent of the variation from 1946 to 1968. Year-classes in excess of 100 million pounds (45,000 metric tons) at age 1, occurred in only 9 of the 41 years. In only one of these 9 years was the spawning biomass below 100 million pounds (57 million pounds). The spawning biomass exceeded 100 million pounds in 24 of the 41 years. This suggests that strong year-classes are most likely to be produced in years with good environmental conditions and a large spawning biomass. It also suggests that given a reasonably large spawning biomass the principal limiting factor in recruitment is not a density-dependent factor. When either a heavy fishery or a series of years with unfavorable environmental conditions occurs (and particularly when both occur together) the future spawning biomass is likely to fall to levels where even optimum environmental conditions cannot produce a strong year-class. In these situations the spawning biomass becomes the limiting factor. In the California Current stock the critical spawning biomass of Pacific mackerel appears to be around 20 to 30 million pounds. With this level of spawning biomass a strong year-class could occur only with the very best environmental conditions. At spawning biomass levels above this critical level recruitment will be progressively less influenced by the spawning biomass level. However, the pattern of variation of the annual environmental conditions appears to be the factor which has the greatest control over the Pacific mackerel population.

There has been much discussion of the role of the "critical period" in the determination of year-class strength. The term "critical period" has been used to cover what we feel are two distinct processes in larval survival of pelagic fishes. The first is the "critical period" in the usage of Hjort (1926), the period just after the yolk sac is absorbed. It is best characterized as time of first feeding. Density-dependence, within the cohort, is not likely to be of great importance to survival through first feeding or until the larvae are several weeks old and greatly increase their mobility. The total number and concentration of eggs in a single spawning spot will affect early survival within the individual spawning spot. During the early larval period mortality of larvae will be dependent primarily upon the following factors:

1) The amount and type of plankton in the immediate proximity of the spawning spot.
2) The concentration of planktonic predators in the vicinity of the spawning spot.
3) Predation by nekton.

The first two factors have undoubtedly contributed to selection for an optimum size and density of individual spawning spot. The larvae in this optimum spawning spot must be dense enough to satiate planktonic predators and sparse enough to insure that the density of planktonic food is sufficient to allow feeding and growth through the early, relatively non-mobile larval stages. Density-dependence in the survival of a cohort through this early feeding stage is likely to be a function of the combined biomass of the entire trophic level. If the biomass of small pelagic fishes is large in relation to the amount of plankton present prior to spawning the plankton concentration is likely to be too low to allow good larval survival and therefore a poor year-class will result. Cushing (1974) has suggested that density dependence within their trophic level is a major factor in the sardine-anchovy relationship in the California Current.

The above considerations have, in our opinion, selected for a reproductive pattern for Pacific mackerel (and other pelagic fishes in upwelling regions) in which the size of spawning schools is much smaller than the size of schools during the rest of the year. Little is known of the spawning behavior and spawning school size in mackerel; however, ripe fish are extremely rare in the commercial landings and purse seiner catches have traditionally been very small during the peak of the spawning period. Thus, it appears likely that optimum spawning school size is relatively small, at least too small to justify a purse seine set.

Lasker (1975–1978) has suggested that virtually all of the survival of first-feeding anchovy larvae is linked to relatively rare patches of suitable-sized phytoplankters. He also observed that chlorophyll maximum layers that contain phytoplankters of suitable size for first-feeding anchovy larvae are likely to be completely dispersed by a single storm. This observation implies that survival through the first feeding could be heavily influenced by the periodicity of individual upwelling events. Closely spaced storms, while providing sufficient nutrients for rapid phytoplankton growth, may prevent the development of the dense concentrations of phytoplankters required for first-feeding larvae. Upwelling events followed by a week to 2 weeks of relatively calm weather may therefore be a requirement for good survival through first feeding. If the interval between upwelling events is too great, total production will be lowered and the survival of older larvae will be reduced.

The second mechanism affecting larval survival occurs during the late-larval and post-larval stages, when the fish are mobile enough to allow mixing between the survivors from different, more widely separated spawning spots. Mackerel in these developmental stages would be able to swim only relatively short distances and their distribution would still be heavily dependent on prevailing surface currents. During this period density-dependent mortality could be grouped into the following categories:

1) Mortality dependent upon density within the cohort. Such mortality may be of two types.
    a) Mortality resulting from competition for the same food source. This type of mortality could conceivably result in a recruitment function similar to the Ricker model where a very large biomass can result in poor recruitment.
    b) Intraspecific predation of eggs and larvae spawned late in the

spawning season by the survivors from earlier spawning. This type of mortality would reduce the number of recruits-per-spawner but is not likely to reduce total recruitment. Mortality of this type is likely to result in a recruitment function of the type used by Cushing (1971).

2) Mortality dependent upon density within the species (i.e., older cohorts).
3) Mortality dependent upon the biomass of the entire trophic level.

Because of their relatively large mouth, late-larval and post-larval mackerel probably feed on larger particle size food than the anchovy or sardine larvae. However, with present knowledge it is probably impossible to make a comparison between the food of these mackerel and pre-adult or adult mackerel. Pre-adult and adult anchovies and sardines undoubtedly feed on the same food organisms as post-larval mackerel. The amount and density of food available to late and post-larval mackerel is dependent on relationships between the production of plankton and the grazing of plankton by organisms at the same or lower trophic levels as the mackerel. It is difficult therefore to separate items 2 and 3 above.

Environmental-dependent mortality will be principally determined by primary production prior to and during the larval stages and upon surface transport of the fish during their relatively non-motile stages. Thus upwelling, divergence-convergence patterns, and geostrophic flow will heavily influence the proportion of prejuvenile fish that will contribute to the recruitment of Pacific mackerel in the California Current Region.

The use of the term environmental-dependent mortality does not necessarily imply that this mortality is either density independent or density dependent. For example mortality of larvae may be greater during a spawning season with reduced upwelling and the mechanism of this mortality may be density related. Conversely, transport of larvae out of the California Current area could be entirely density-independent. It should be emphasized that recruitment is an interplay between environmental factors and spawning stock size and therefore density-independent fluctuations and density-dependent relationships are not separate halves of the process.

The large environmentally related fluctuations in recruitment of Pacific mackerel suggest that the recovery of the stock is more likely to be related to environmental conditions than to the resiliency of a population that is under carrying capacity. The resiliency could be further reduced if a depensatory mortality factor becomes significant. Clark (1974) suggested that a depensatory factor could be associated with the collapses of the populations of pelagic schooling fishes. The mechanism suggested by Clark, increased mortality due to a reduction of the size of schools, is not likely to result in critical depensation because the Pacific mackerel subadults and adults commonly school with jack mackerel. A second mechanism, increased larval mortality due to suboptimum spawning school size, could result in critical depensation and long-term loss of the stock.

COMPUTER SIMULATIONS

SIMULATION MODELS

The computer simulation models used in this work were written in FORTRAN IV and were run on a CDC 6500 computer. Two simulation models were used. The simpler model (ISOE, Appendix I) is a yield-per recruit model based on the yield equations described by Beverton and Holt (1957) and as revised by Ricker (1975). ISOE calculates the relative yield from a cohort at various combinations of exploitation rate and age at recruitment to the fishery.

The ISOE program calculates yield matrices for 1000 weight units of recruits. The matrices are output with the exploitation rates (and instantaneous fishing mortality rates) on one axis and age at recruitment on the other axis. The program is run with user supplied increments of exploitation rate and the instantaneous fishing mortality rates are calculated with an iterative solution based on Newton's method. User supplied input includes the maximum age of the species, the proportion spawning by age group, the Bertalanffy growth equation constants, the length-weight equation constants, the minimum and maximum ages at recruitment, and the exploitation rates for which the simulation is run.

The second simulation model (QUOTAE, Appendix II) was developed to simulate the Pacific mackerel population under a quota system similar to the present California regulations governing the fishery. QUOTAE is a dynamic pool model and includes a spawner-recruit function. This model combines many of the ideas used by Walters (1969) and Allen (1973). QUOTAE calculates the mean yield over a period of years with various combinations of quota proportion and age at recruitment. The quota proportion is defined as a fraction of the stock above some minimum level. The minimum level in the case of the California Pacific mackerel regulations is the spawning biomass level at which a moratorium on commercial fishing comes into effect (i.e., 20 million pounds). In the case of salmon the minimum level might be the minimum escapement.

The program can be run with no minimum biomass level, with a minimum biomass level or with a lower biomass level and an upper biomass level. In the first option the quota proportions are identical to exploitation rates. The second option allows increments of the quota proportion above the minimum biomass level. The third option is patterned after the California regulations and also resembles the approach followed by Allen (1973). As used in the Pacific mackerel simulations the third option would have a lower biomass level of 20 million pounds, a lower quota proportion of 0.2, an upper biomass level of 40 million pounds, and an upper quota proportion that is varied to determine the yields under different quota proportions.

In fisheries where the estimates of recruit biomass are measured at essentially the same time as those of spawning biomass the spawner-recruit curve can be used as an excess production curve. This is the case in some salmon fisheries. In most fisheries this is not the case. Recruitment occurs at some intermediate age and each cohort is exploited over a period of years. Thus for most fisheries the shape of the excess production curve is influenced by both the exploitation rate and the age at recruitment. If environmental factors cause considerable variation from a spawner-recruit function the surplus production curve will also show considerable variation. The QUOTAE model can be used to evaluate the yields under the various surplus production curves resulting from different management policies. This includes policies based on equilibrium yield that use a density-dependent spawner-recruit function. It also allows assessment of yields under a recruitment function that includes both environmental and density-dependent factors. In the latter case the model can be either deterministic or stochastic.

Biological input to the model included growth and proportion spawning by age group, a recruitment function, and natural mortality. Annual growth and growth to capture were the growth proportions calculated with the ISOE program. These calculations were made with the Bertalanffy and length-weight equations presented by Knaggs and Parrish (1973). The proportion spawning by age group was the data discussed earlier and the proportion of age 1 spawners was density-dependent. The natural mortality and fishing mortalities were not age specific and an instantaneous natural mortality of $M = 0.5$ was used in all simulations. Spawner-recruit functions used in the simulations will be presented later and they included density-dependent functions and density-environmental-dependent functions. In several of the environmental-dependent recruitment functions the response to the environmental variables is determined by the age structure of the spawning biomass.

The normal output of QUOTAE consists of yield matrices for the mean yield over the period of the simulation and the yield in the last year of the simulation. The yield in the last year of the simulation is used for equilibrium recruitment functions. Output options include the output of annual spawning biomass, total biomass, recruitment, and yield for each age at recruitment and upper quota proportion. Control card options include the following:

1) Alteration of the quota levels and proportions used to calculate the annual quota.
2) The quota can be based on either the spawning biomass, total biomass, or the combined biomass of one-year-olds and two-year-olds.
3) A percentage catch of undersized fish can be set.
4) The proportion of a year-class that spawns can be density-dependent.
5) The environmental variables used in the recruitment function can be weighed by the proportion of the biomass that spawns during different periods of time.

For specific details the reader is referred to Appendix II.

YIELD-PER-RECRUIT MODEL

Yield-per-recruit isopleths were calculated an instantaneous natural mortality rate (M) of 0.5. Von Bertalanffy growth data were the previously discussed coefficients from Knaggs and Parrish (1973). Our program used also calculates matrices of resultant spawning biomass per unit weight of recruits. A generalized version of the program is listed in Appendix I. The proportions of mature fish by age group used for these calculations were 0.26, 0.77, 0.88, and 1.0 for age groups 1, 2, 3, and 4+. Maximum age was 11 (Fitch, 1952).

The maximum yield per unit weight of recruits is dependent upon the choice of natural mortality. The maximum in each case occurred with an age at recruitment of one or less and with F = 1.0, the highest instantaneous fishing mortality rate used (Figure 20). The low age at recruitment for maximum yield is consistent with the species biomass curve with age (Figure 21). This curve shows that when there is no fishing mortality, biomass peaks when the fish are yearlings. Several workers (Walters 1969, Ricker 1975:241) have suggested that the best policy is to harvest each cohort close to the age when biomass loss through mortality balances biomass gain through growth, subject to the constraint that adequate reproduction is maintained.

A fishery operating at the high fishing rates and low age at recruitment necessary to achieve maximum yield-per-recruit in Pacific mackerel results in a situation that produces a minimum spawning biomass from a ton of recruits. Under this fishing strategy, spawning biomass per recruit is less than ¼ of that which occurs with no fishery (Figure 20B).

EQUILIBRIUM YIELD SIMULATIONS WITH DENSITY-DEPENDENT RECRUITMENT

The QUOTAE model was run with several of the density-dependent recruitment functions previously described. The first series of simulations used the linear and nonlinear regression fits to the Ricker and Cushing spawner-recruit functions (Table 17). In these simulations the quota was based on the total biomass and the quota levels were set at zero. Therefore, in these simulations the model calculates the exploitation rates. The second series of simulations was run at various quota levels and the quota was based on the spawning biomass. This series utilized only the Ricker nonlinear regression function. This function was chosen because it has the highest predictive capability. All of the above simulations were run with the 1931 biomass as the starting population. The simulations were run with 5 age at recruitment levels and 20 exploitation rates. The simulations were run for 100 years and the equilibrium yield was taken to be the yield in the 100th year. Simulations with all of the above models had stabilized by the 12th to the 50th year. Yields during the 90th to 100th year varied less than 0.001% with each of the above models.

Equilibrium yield isopleths for the Ricker and Cushing recruit-spawner models show the same similarity as previously described in the spawner-

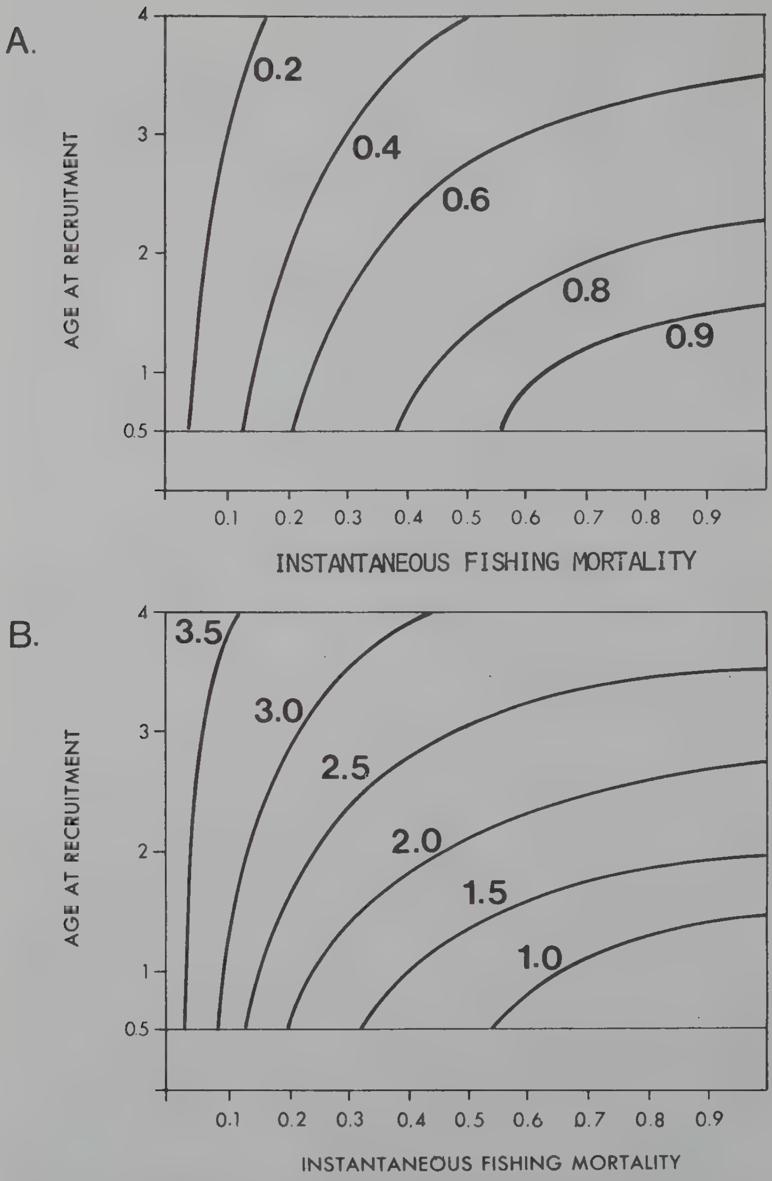

FIGURE 20. Isopleth model with M = 0.5; A. Yield per unit weight of age 1 recruits; B. Resultant spawning biomass per unit weight of age 1 recruits.

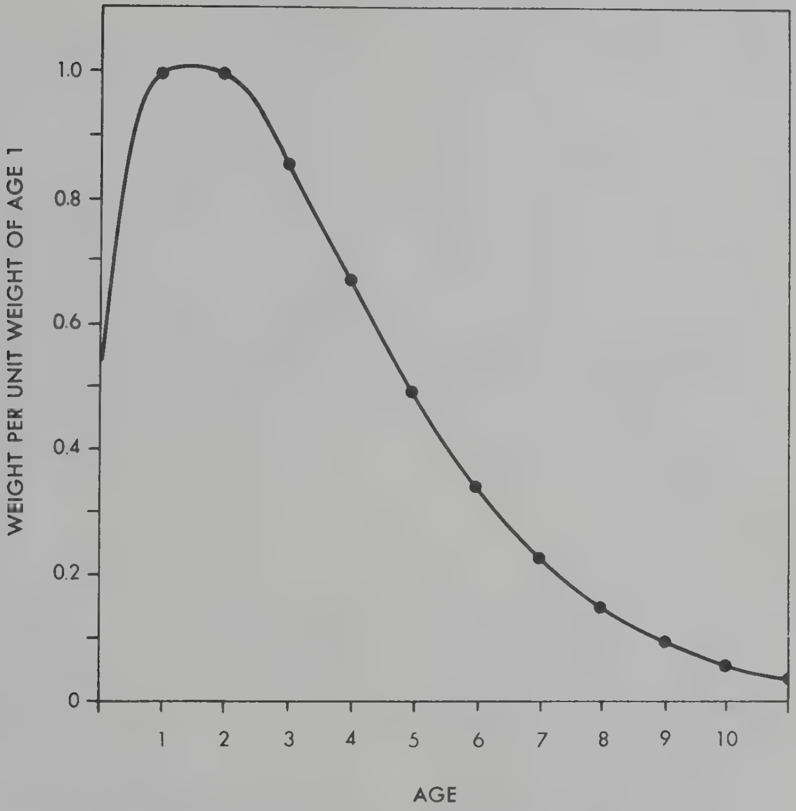

FIGURE 21. Pacific mackerel biomass curve with no fishery and M = 0.5.

recruit curves (Figure 22). The linear fits to the Ricker function and the Cushing function produce similar yield isopleths and the nonlinear fits also produce similar isopleths. The linear regressions with the Ricker and Cushing functions have a bias towards low estimates as they utilize log transformed variables. This bias is evident in the low equilibrium yields predicted by the isopleths calculated with the linear regression spawner-recruit functions. Average observed yield from 1931 to 1968 was 49 million pounds (22,000 metric tons).

The recruitment functions fitted by linear regression predict that maximum yield will occur with an age at recruitment of above age 4 and at low exploitation rates. Maximum equilibrium yield with an age of recruitment of 1 is with exploitation rates of around 0.15 to 0.3.

The recruitment functions fitted with nonlinear regressions predict that maximum equilibrium yield will occur with an age at recruitment of between 3 and 4. At this age and with exploitation rates in excess of about 0.2, the Ricker nonlinear function predicts equilibrium yields above 80

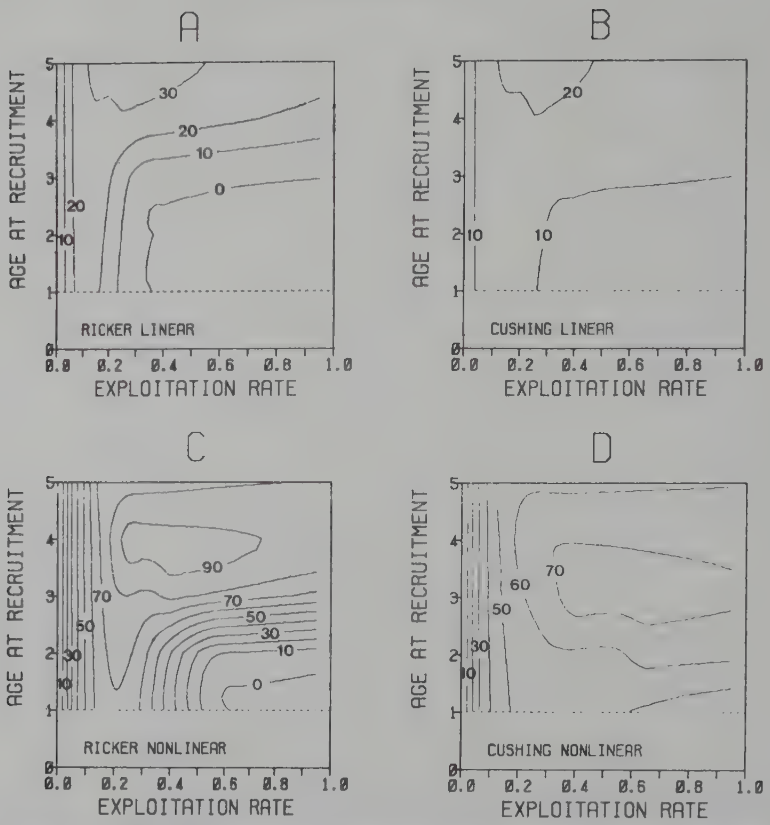

FIGURE 22. QUOTAE equilibrium yield isopleths with density-dependent spawner-recruit functions (Yield in millions of lbs)

million pounds; (36,000 metric tons) and the Cushing nonlinear function predicts yields above 60 to 70 million pounds (27,000 to 32,000 metric tons). High exploitation rates show little reduction in yield at an age of recruitment of 3 to 4. It should be noted that the Ricker functions predict that extinction will occur if the age at recruitment is 1 or lower and the exploitation rate exceeds 0.6. It has been shown that during the population collapse of the late 1960's the exploitation rate on the Pacific mackerel exceeded 0.6 and the age at recruitment was less than age 1 (Parrish, 1974).

Equilibrium yield simulations with four different sets of quota levels show little difference in yields at upper quota proportions below 0.4 (Figure 23). When the upper quota proportions are above 0.5 and the age at recruitment is 1 or 2 the equilibrium yield is markedly depressed in the simulation with the quota levels set at zero (Figure 23A). The maximum equilibrium yield with all four sets of quota levels occurs at an age of recruitment of around 4 and with an upper quota proportion of above 0.4.

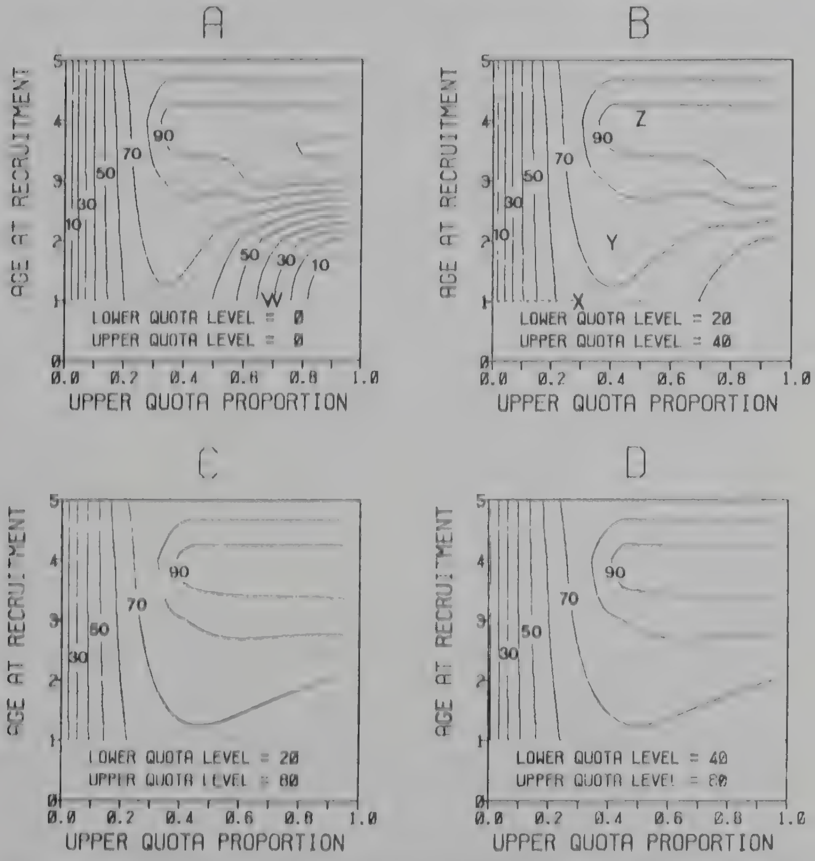

FIGURE 23. QUOTAE equilibrium yield isopleths, at four different sets of quota levels with the Ricker nonlinear model (Yield in millions of lbs, quota based on spawning biomass)

The present California regulations controlling the Pacific mackerel fishery consist of quota levels and lower quota proportion as in Figure 23B and an upper quota proportion of 0.3. The age at recruitment during most of the observed fishery was age 1. This location in the yield isopleth is shown by the symbol X. This series of simulations suggests that, if environmental factors are not considered, the quota levels and quota proportions in the California regulations are properly set from an equilibrium yield philosophy. The simulations suggest that the yields could be increased by enforcing a strict size limit. It would be impossible to achieve maximum equilibrium yield with the present purse-seine fishery but it could be achieved by a return to the scoop fishery, which could technically be controlled to reduce greatly the catch of fish less than 3 years old.

YIELD WITH ENVIRONMENTAL-DEPENDENT RECRUITMENT FUNCTIONS

Two series of simulations were made with the QUOTAE program and environmental-dependent recruitment functions. The first series utilized the nonlinear Ricker sea level function (Table 19). These simulations started in 1931 with the observed 1931 biomass, by age group, and ran through 1968. The second series used the nonlinear Ricker transport recruitment function, the 1946 starting biomass, and ran through 1968.

The above simulations were run in a manner that differs from the way such simulations are normally run. In most fisheries models environmental variation in recruitment is considered to be a random process (Allen 1973, Walters 1975). Simulations are therefore usually run with a stochastic environmental term. The driving stochastic variable is usually picked from either a distribution with the same mean and variance as the observed environmental variation or from a distribution with a mean of zero and a variance the same as the observed variance from some recruitment function. Variation in recruitment of Pacific mackerel is markedly nonrandom; instead it shows an aperiodic cyclic pattern. This pattern can be seen in a time series of the natural log of the number of observed recruits per spawner (Figure 9). Because of the nonrandomness of recruitment it was decided that a more realistic assessment of the effects of alternative management policies would be obtained by using the observed environmental data to generate recruitment. For example, the simulations with the nonlinear Ricker transport function were run with the observed April, May and June mean values for the upwelling indices and offshore divergence indices at 30°N.

The similarity of the yield isopleths in four simulations with the nonlinear Ricker sea level function and varying quota levels suggests that long-term yield is not very sensitive to alterations in the quota levels (Figure 24). Mean yield also appears to be independent of age at recruitment at upper quota proportions below 0.3. At upper quota proportions above about 0.4 mean yield is influenced by age at recruitment and maximum mean yield occurs at high upper quota proportions and an age at recruitment of about 3 years.

The 1946–1968 series of simulations made with the nonlinear Ricker transport recruitment function and the same quota levels as the previous series do not show that yield is greatly influenced by age at recruitment (Figure 25). When the quota levels are set at zero, mean yield is almost entirely dependent on the quota proportion. The exception to this is that when the quota proportions are above 0.3 the mean yield is less when age at recruitment exceeds age 3. When the upper quota level is set at 80 million pounds (36,000 metric tons) the simulations suggest that mean yield is low, around 10 to 15 million pounds (4,500 to 6,800 metric tons) over the entire range of age at recruitment and the entire range of quota proportions.

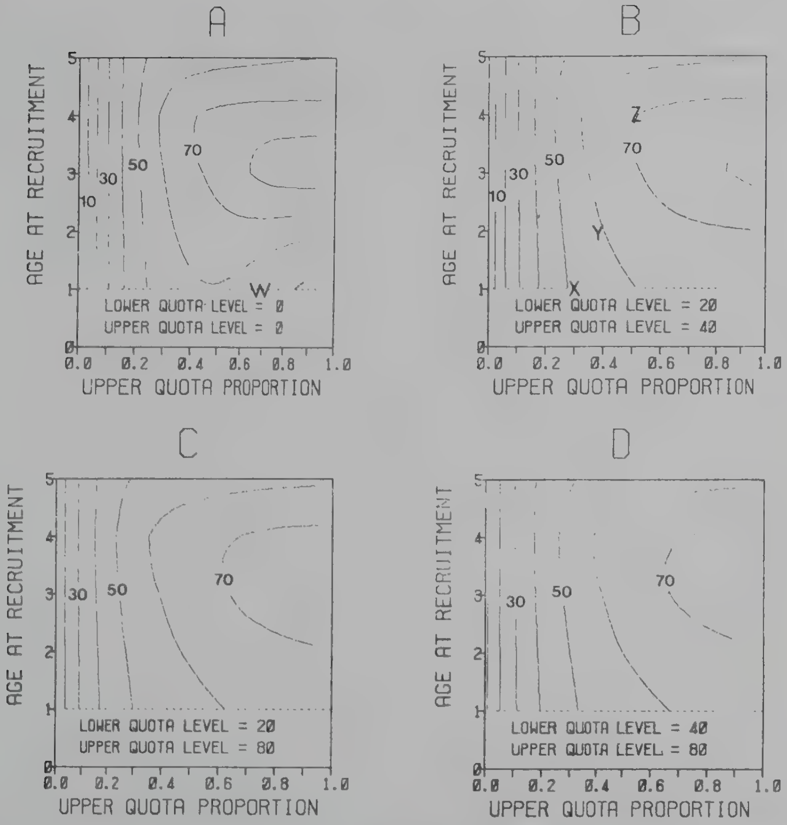

FIGURE 24. **QUOTAE mean yield isopleths (1931–1968), at different sets of quota levels, with the Ricker sea level model. (Yield in millions of lbs, quota based on spawning biomass)**

The preceding simulations with the two environmental-dependent recruitment functions show considerable difference in mean yields. There are several reasons for this. First the recruitment functions were fitted to different time periods; the sea level function was fitted to data from 1931–1968 and the transport function included data from 1946–1968. The transport function was fitted to data with a much lower mean spawning biomass; and in addition, about half of the years from 1946–1968 were during the periods of the sharp population declines that occurred during the early 1950's and the mid 1960's. The simulations also differ in that the starting biomass for those with the sea level function used 1931 as a base while the transport simulations started with 1946. The 1931 biomass was about 4.7 times larger than that of 1946 (611 vs 131 million pounds, 277,000 vs 59,000 metric tons). This factor of course resulted in higher mean yields in the simulations which started with the 1931 biomass.

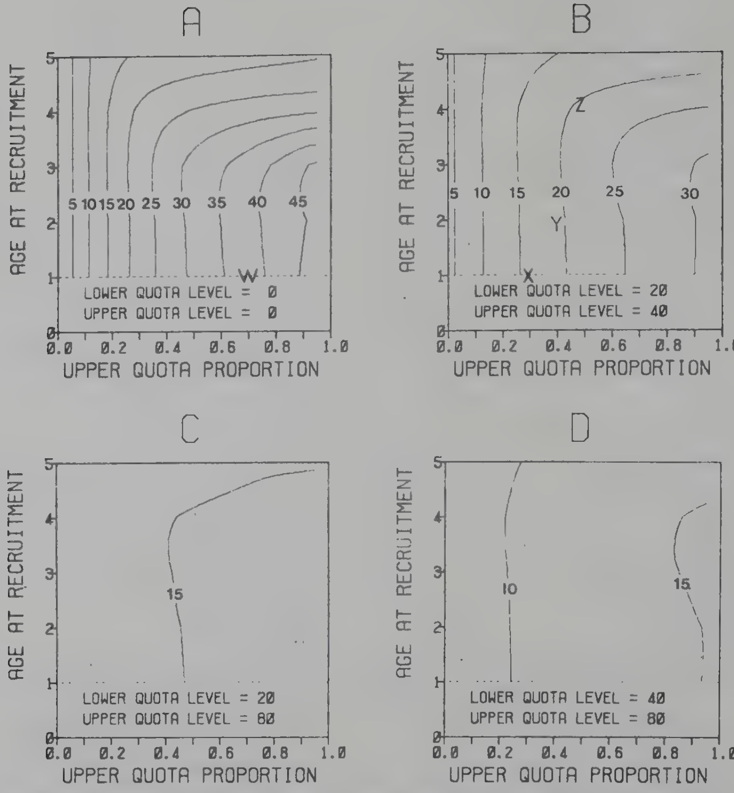

FIGURE 25. QUOTAE mean yield isopleths (1946–1968), at four different sets of quota levels, with the Ricker transport model (Yield in millions of lbs, quota based on spawning biomass)

ANNUAL YIELD UNDER FOUR MANAGEMENT OPTIONS

To assess the similarity of yields under the different environment-dependent recruitment functions, simulations under four management options were run. These simulations had the same time periods (1946–1968) and were initialized with the observed 1946 biomass. A third environmental-dependent recruitment function was included in this series of simulations. This recruitment function, the "reduced sea level model," was included to determine if the population decline of the late 1960's would have been predicted by a recruitment function that was fitted to a reduced data set that did not include the period of the population decline.

The major difference between the yield estimates with the density-dependent and environmental-dependent recruitment functions is the large variation in annual yield that occurs in the simulations run with the environmental-dependent recruitment functions. Time series of yields in simulations with the density functions show a stable approach to equilibrium yield. Simulations (1946–1968) with the Ricker sea level functions and the Ricker transport function show considerable variation in annual yield under different management options. Figures 26 and 27 show simulations with the Ricker sea level, reduced Ricker sea level and Ricker trans-

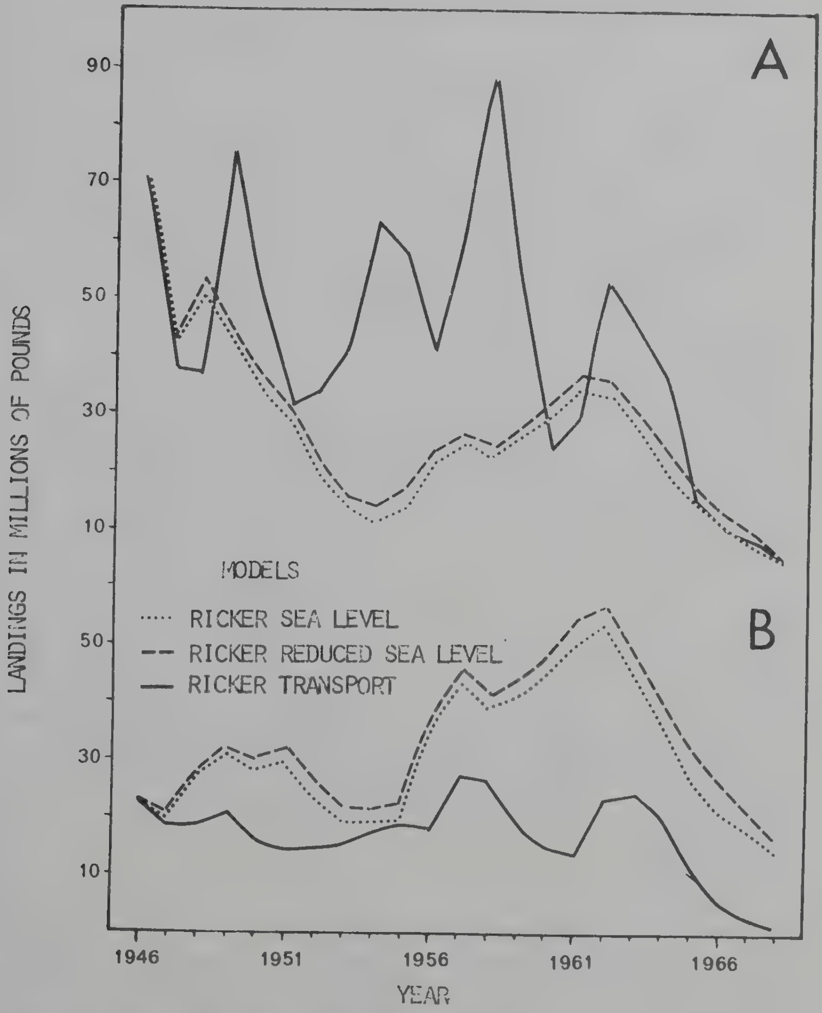

FIGURE 26. **QUOTAE simulations (1946–1968); A. Recruitment at age 1, no minimum quota level and a quota proportion of 0.7 (w in figs 21A and 22A) B. Present California Regulations recruitment at age 1 and an upper quota proportion of 0.3 (x in figs 21B and 22B)**

port recruit functions. Simulations for each recruitment function are shown with four different management options. The first option (Figure 26A) includes fishing rates that approximated those that occurred in the late 1960's. The other three options are based on the California regulations and have lower and upper quota levels of 20 and 40 million pounds (Figures 26B, 27).

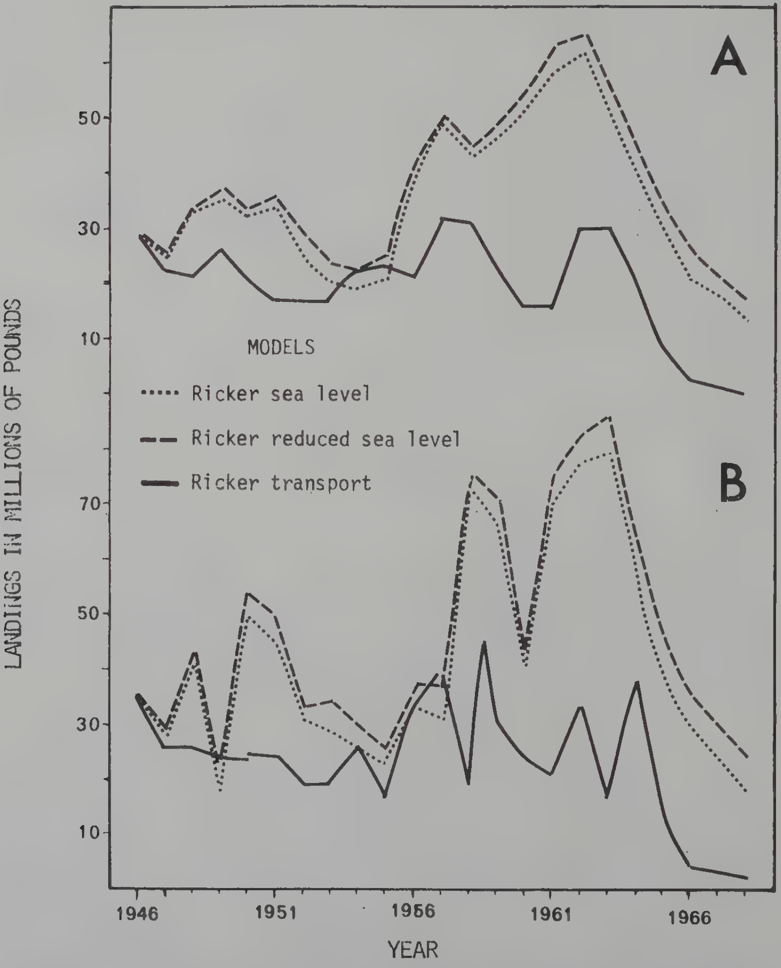

FIGURE 27. QUOTAE simulations (1946–1968); A. Recruitment at age 2 and an upper quota proportion of 0.4 (y in figs 21B and 22B) B. Recruitment at age 4 and an upper quota proportion of 0.5 (z in figs 21B and 22B)

The Ricker sea level and reduced Ricker sea level models show essentially the same yields within each option. Yields with the reduced Ricker sea level model are always slightly higher than those with the Ricker sea level model. The reduced model was fitted to data (1931–1960) with a slightly higher mean recruitment than the Ricker sea level model (1931–1968). The Ricker transport model shows considerably higher yields than the sea level models in the simulations with an age at recruitment of 1 and a quota proportion of 0.7. Yields with the Ricker transport model under the three quota level options are considerably lower than yields with the sea level models and also much lower than yields with the Ricker transport model in the option with a quota proportion of 0.7. The reason for the much higher predicted yields in the transport model with the 0.7 quota proportion is an apparent bias in the compensatory term in the Ricker function. This bias will be discussed later.

The simulations with the sea level models show considerably different yield patterns under the four management policies. For example, the yields in the simulations with an exploitation rate of 0.7 show a sharp decline from 1946 to 1954 (Figure 26A). Yields declined from about 70 million pounds to about 13 million pounds and then rose to about 35 million pounds in 1961 (32,000 to 5,900 to 16,000 metric tons). By comparison, the simulation with the present California regulations, which result in an exploitation rate below 0.3, show yields of between 20–30 million pounds (9,000–13,000 metric tons) from 1946–1954 and a large increase in yields during the 1956–1966 period (Figure 27A). The heavy exploitation and resultant decrease in spawning biomass with the 0.7 quota proportion option decreased the large 1956–1966 increase in yields that is predicted by the simulations with the present California regulations. The simulations with age at recruitment of 4 (Figure 27B) show sharper variations in annual yield than with the other three options. This management option, which protects the spawning biomass, puts a very heavy exploitation rate on the 4-year-olds. With this option almost the entire yield is 4-year-olds and therefore the annual yield is erratic because it is dependent upon individual year classes.

The precipitous decline in the Pacific mackerel population in the late 1960's is evident in all of the simulations with environmental-dependent recruitment functions. The decline went to lower spawning biomass levels in simulations with high exploitation rates; however, low spawning biomass also occurred in the late 1960's in simulations with no fishing mortality.

DISCUSSION

EVALUATION OF RECRUITMENT MODELS AND SIMULATIONS

The poor statistical fits of the density-dependent recruitment functions presented earlier (Table 17) suggests that these models are of limited use for management purposes. They could be used for long-term management purposes (i.e., to estimate long-term yields under a given exploitation rate) but should not be used for real time management. The recruitment models that include both density-dependent and environmental-dependent components (Table 19) are considerably better than the density-dependent recruitment functions in predicting recruitment in a given year. Two important questions remain. How good are the environmental models? Are the variables in the models good indices of the real mechanisms that control recruitment.

The transport models have the best statistical fits; however, they are deficient in the sense that they were fitted to a shorter data series than the sea level models. This shorter series (1946–1968) did not include any years in which the spawning biomass was at the high levels that occurred prior to the peak of the fishery in 1936. Mean recruitment during the 1946–1968 period was considerably smaller than during the 1931–1968 period. The transport models therefore were fitted to a data series that is biased towards low recruitment. The computer simulations presented earlier show that the Ricker transport model predicts considerably smaller recruitment and yields than the Ricker sea level models and the density-dependent Ricker and Cushing models. The low estimates are not caused by the environmental terms. The low recruitment estimates with the Ricker transport model are caused by the compensatory term of the Ricker model. The 1946–1968 and 1928–1968 linear fits to the Ricker spawner-recruit model have very great differences in their density-dependent and compensatory terms.

1946–1968 $R = 1.123Pe^{0.0000169\ P}$

1928–1968 $R = 0.508Pe^{0.00000214\ P}$

The 1946–1968 model has a much steeper ascending curve and the compensatory term is important at much smaller spawning biomass levels. The 1946–1968 model predicts greater recruitment at low spawning biomass levels than does the 1928–1968 model. Thus the simulations with the Ricker transport model have greater yields than the Ricker sea level models when the exploitation rate is very high (Figure 26B)and smaller yields when the exploitation rate is moderate (Figures 26B, 27). The compensatory term (e^{bP}, Table 16) for several spawning biomass levels is shown below for the nonlinear Ricker, Ricker sea level and Ricker transport models.

	Ricker	*Ricker sea level*	*Ricker transport*
Compensatory Term (CT)	$e^{-0.00000253 P}$	$e^{-0.00000353 P}$	$e^{-0.0000377 P}$
Spawning biomass in millions of Pounds			
20	CT = 0.951	CT = 0.932	CT = 0.470
50	CT = 0.881	CT = 0.838	CT = 0.152
100	CT = 0.776	CT = 0.703	CT = 0.023
200	CT = 0.603	CT = 0.494	CT = 0.0005
400	CT = 0.363	CT = 0.244	CT = 0.0000003
600	CT = 0.219	CT = 0.121	CT = 0.00000000015

The above data demonstrate a major difficulty in developing regression models to describe the spawner-recruit relationship in exploited populations. Such regression models are generally lacking in data at the high spawning biomass levels that typically occur before exploitation begins. The compensatory term of the Ricker transport model is a good example of the unrealistic, yet statistically valid, regression models that can result from regressions based on data sets which do not include a good representation of data from the entire range of population biomass.

Further work that would incorporate upwelling and offshore divergence indices back to 1928 is envisioned. Barometric pressure fields are available back into early 1900's. The use of these pressure fields to calculate upwelling and offshore divergence indices will soon be in progress and further refinement of the transport models is dependent on this longer data series.

We feel that the environmental variables in the transport model (Bakun's upwelling and wind stress curl indices) are more direct estimates of the mechanisms that regulate recruitment than are the variables in the sea level models. Upwelling is obviously related to recruitment, because it determines the basic productivity of the California Current Region. Bakun and Nelson (In Press) have suggested that strong, negative wind stress curl (convergence) at 30°N would contribute to the separation of the surface waters north and south of the Punta Eugenia area. Weak, negative wind stress curl would be associated with an increase in the mixing between the two areas. Their hypothesis has several interesting features. It describes a physical boundary that explains the presence of the separate stocks of Pacific mackerel, sardine and anchovy that are found north and south of central Baja California. It also suggests that larvae from a wider geographical area could contribute to the California stock during periods of weak convergence at Punta Eugenia. A second hypothesis is that strong convergence at 30°N in the center of abundance of Pacific mackerel could be inhibitory to survival of Pacific mackerel larvae. Either downwelling or the formation of fronts conceivably could result in increased larval mortality.

The sea level models do not have as good statistical fits as do the transport models; however, they are fitted to data that include the entire range of observed spawning biomass. The environmental variables in the sea level model (sea level, barometric pressure and sea surface temperature) are correlated with the real environmental variables that control recruitment, but with the exception of sea surface temperature they are not direct estimates of the real variables.

Sea level at La Jolla during the spawning season is negatively correlated with recruitment. Hicks and Crosby (1974) have shown long-term increases in sea level at La Jolla and San Diego. The trend in increasing sea level could be caused by land subsidence in the La Jolla-San Diego area or a wide range of oceanographic and atmospheric factors. It is possible that the negative correlation is affected by the opposing trends of increasing sea level and decreasing population of Pacific mackerel that occur over the 1928–1968 period. Of course, this trend would not account for the seasonal pattern of correlation coefficients.

The decadal differences in sea level, between 1948–1957 and 1958–1969, at San Diego were analyzed by Huang (1972). He suggested that geostrophic flow provided the major contribution to the differences in sea level. High correlations between geostrophic flow and sea level were also found during the Coastal Upwelling Experiment (CUE); increased southward flow was associated with decreased sea level (Smith, 1974). It therefore appears that the correlation between ln(R) and sea level is a measure of the underlying relationship between recruitment in Pacific mackerel and geostrophic transport. Increased geostrophic flow in the California Current would be expected to increase the southerly advection of nutrient- and plankton-rich water from the major upwelling regions off of central and northern California. Therefore the survival and growth of larvae in the Southern California Bight and Baja California region should be enhanced by increased geostrophic flow.

Barometric pressure is a measure of atmospheric circulation, and low barometric pressure at San Diego is associated with increased winds in the southern end of the California Current. Barometric pressure is therefore an index of upwelling in this region.

The positive correlation between sea surface temperature and recruitment is expected. Warm SST should favor recruitment in the California Current stock of Pacific mackerel, because this stock is on the cold-water edge of its potential range. However, this correlation would seem to be in contradiction with the correlation between upwelling and recruitment. If increased upwelling occurs during the spawning season SST should be reduced. It is possible that SST is influenced by the spacing of upwelling events, being lower if upwelling is more continuous and higher if upwelling events are followed by periods of calm weather with considerable isolation (a condition that should favor recruitment). Upwelling prior to the spawning season would also tend to decrease SST and possibly increase the number of planktonic predators. Large scale SST anomalies unrelated to upwelling in the northern Baja California area could also increase SST in this area.

Simulations with the density-dependent recruitment functions predict that at high exploitation rates equilibrium yield is quite sensitive to changes in the age at recruitment. Maximum yield with the nonlinear Ricker and Cushing spawner-recruit functions occurs at exploitation rates above 0.3 and at an age of recruitment of between 3 and 4 years of age. If the fishery were to be managed with the present California regulations, the Ricker function predicts that equilibrium yield would be about 67 million pounds (30,000 metric tons) per year (X in Figure 23B). The simulations suggest that equilibrium yield could be increased to over 95 million pounds (43,000 metric tons) if the upper quota proportion were increased to 0.5 and the age at recruitment increased to age IV (Z in Figure 23B). This large an increase in potential yield is not predicted by comparable simulations with the environmental-dependent recruitment functions. Simulations with the sea level spawner-recruit function predict that mean yield for the period of 1931–1968 would have been just over 51 million pounds (23,000 metric tons) if the present California regulations had been in effect over this period (X in Figure 24B). Observed yield for this period averaged 49 million pounds (22,000 metric tons). The above simulation predicts that mean yield would have increased to 69 million pounds (31,000 metric tons) if the quota proportion had been set at 0.5 and the age at recruitment had been IV (Z in Figure 24B). However, yields would fluctuate more. The highest age at recruitment that could be considered practical for the Pacific mackerel fishery is age 2. This is due to the mixed schooling of different age groups of mature Pacific mackerel. When the age at recruitment is set at age 2 the equilibrium yield with the Ricker Model is a maximum of 75 million pounds (34,000 metric tons) at an upper quota proportion 0.4 (Y in Figure 23B). The Ricker sea level model predicts that the mean yield under this management (Y in Figure 24B) would have been 60 million pounds (27,000 metric tons).

The Ricker sea level model predicts that the mean annual yield over the period of 1946–1968 would have been 31 million pounds (14,000 metric tons) if the California regulations had been enacted in 1946. The observed mean yield over this period was 31 million pounds. Mean yield over this period with an age at recruitment of 2 and an upper quota proportion of 0.4 is predicted at 35 million pounds (16,000 metric tons). The corresponding predictions with the Ricker transport model (Figure 26) are 16 and 19 million pounds (7,200 and 8,600 metric tons).

It appears that the simulations with the Ricker sea level model are more realistic than those with the Ricker transport model. Yields with the environmental models are considerably lower than those predicted by the equilibrium simulations with the density-dependent recruitment models. The yield-per-recruit simulations (ISOE) predict that maximum yields on an individual cohort occur at an age at recruitment of less than 1 and at high fishing mortality rates. Spawning biomass levels with this management policy are minimal and long term yield under this policy is low in both the equilibrium and environmental-dependent simulations with the QUOTAE program.

The predictive capability of recruitment in a given season is highest with the transport models. The Ricker transport model accounts for over 75% of the variation in recruitment for the period of 1946–1968. It would be desirable to test the predictive capabilities of the various recruitment models with data from years outside of the period for which the models were fitted. Unfortunately good quality population estimates are not available for the period of 1970–1975. This lack of data was caused by the moratorium on the commercial fishery. The moratorium halted the market sampling program from which age composition data were derived. Estimates of the population size and recruitment for the 1970–1975 period therefore cannot be based on a cohort analysis. Available estimates on the recent spawning biomass are based on small scale tagging studies, and estimates of recruitment during the 1970–1975 period are not available. However, the environmental portion of the Ricker transport model predicts that from 1963 to 1975 there were no years in which the environmental conditions greatly favored recruitment. Moderately good environmental conditions were predicted in 1971, 1972 and 1974.

ALTERNATIVE MANAGEMENT PLANS

Pacific mackerel management policies that could be developed with the several modeling approaches contained in this study vary considerably. Policies based on yield-per-recruit simulations would favor the very high exploitation rates and an age at recruitment of 1 or less that are necessary to achieve maximum yield per recruit. Equilibrium yield simulations based on the Cushing or Ricker spawner-recruit models suggest that near maximum sustained yield (MSY) would be achieved with a wide range of exploitation rates ($E = 0.3$ to 0.6) and an age at recruitment of age 3 or 4. With a management policy based on a maximum yield per recruit philosophy equilibrium yield simulations based on the Ricker spawner-recruit model predict that the stock would become extinct. Similar simulations with the Cushing spawner-recruit model predict that yields would be well below MSY.

Simulations with a wide range of quota options and the environmental-dependent recruitment models suggest that no management policy is likely to stabilize the yield at reasonably high levels. The best management policy therefore appears to be one that will reduce the possibility of future population collapses and at the same time achieve a maximum long-term yield. That is a policy that will reduce the exploitation rate when the population level is low and increase the exploitation rate when the level is high.

Determination of the optimum management policy will require considerable economic analysis and is therefore beyond the scope of the present work. However, in the absence of such analyses we feel that the list of potentially optimum management policies can be reduced to three alternatives. These alternatives are maximum long-term yield with an age at recruitment of 1, 2, or 3. Maximum long-term yield is likely to be close to optimum yield because of a combination of biological and economic factors. The stock is a member of a multispecies wetfish fishery and it is of secondary importance in this fishery. The stock is readily available to the fishery and the fishing fleet has demonstrated that it is capable of harvesting Pacific mackerel at rates in excess of their reproductive potential. The economics of the fishery are primarily dependent upon relationships with the more abundant species in the fishery (i.e., presently anchovy). In addition the price for Pacific mackerel has traditionally been higher than the price for the more abundant species in the fishery. Therefore, economics are unlikely to be the limiting factor in the Pacific mackerel fishery and maximum economic yield may approach maximum biological yield.

The three alternative management policies (Table 20) are based on the quota proportions that resulted in the maximum predicted long-term yield with an age at recruitment of 1, 2 and 3. All three management policies contain portions of the present California regulation. Specifically they maintain the present moratorium, or lower quota level, at 20 million pounds spawning biomass to ensure a viable sport fishery. They have a lower quota proportion of 0.2 and an upper quota level of 40 million pounds to allow only a minor fishery when the spawning biomass is relatively small.

The success in describing past recruitment in Pacific mackerel with statistical fits to environmental and population data does not prove that the factors found to be associated with recruitment are those that control recruitment. It is also possible that these environmental factors may not continue to be associated with recruitment in future years. The tentative decision to accept the hypothesis that recruitment can be predicted with more accuracy if the associated environmental factors are taken into consideration should only be made if the environmental factors make biological sense. We believe that a very strong case can be made that the

TABLE 20 Alternative Management Options *

Management Option 1. The present California regulations.

No minimum size restrictions
Quota levels of 20 and 40 million pounds
Lower quota proportion of 0.2
Upper quota proportion of 0.3
Predicted long-term yield
  50 million pounds per year
  22,600 metric tons per year
  $2,260,000 per year at $100 per short ton

Advantages
  Status Quo
  Least amount of regulation of the fishery

Disadvantages
  Long-term yield is the lowest of the 3 options
  Age structure will be the most altered

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* It should be noted that the alternative management options are for the total catch, including the sport and commercial fisheries of Mexico and California

Management Option 2. Compromise option

Minimum size restriction to protect 1 year olds
Quota levels of 20 and 40 million pounds
Lower quota proportion of 0.2
Upper quota proportion of 0.5
Predicted long-term yield
  64 million pounds per year
  29,000 metric tons per year
  $2,900,000 per year at $100 per short ton

Advantages
  Long-term yield is increased without precluding a purse-seine fishery

Disadvantages
  Size restriction will increase the fishing effort necessary to catch the quota
  Enforcement costs for minimum size limit.

Management Option 3. Near MSY option

Minimum size restriction to protect 1 and 2 year olds
Quota levels of 20 and 40 million pounds
Lower quota proportion of 0.2
Upper quota proportion of 0.7
Predicted long-term yield
  76 million pounds per year
  34,500 metric tons per year
$3,450,000 per year at $100 per short ton

Advantages
  Largest long-term yield
  Least altered age structure

Disadvantages
  Annual yield is the most variable
  Size restrictions will preclude a purse seine fishery
  Enforcement costs will be the highest

environmental factors found to be associated with recruitment are in fact those that describe major components of the mechanisms that control that mortality of pelagic fish eggs and larvae in the California Current Region.

Management of the fish stocks in the California Current Region must recognize that changing environmental conditions will cause large variations in the recruitment of commercially important species of the California Current. If this factor is not recognized and incorporated in management policies, overfishing very likely will occur during a period of poor recruitment and the list of populations in the California Current that have suffered recruitment failure will include species other than the Pacific sardine and the Pacific mackerel.

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APPENDIX I. YIELD PER RECRUIT SIMULATION PROGRAM.

```
      PROGRAM ISOE (INPUT,OUTPUT,PUNCH)
C     YIELD PER RECRUIT MODEL          RH PARRISH  MAY 10,1976
C     CONTROL CARD VARIABLE DESCRIPTION
C      NRUNS      NUMBER OF RUNS TO BE MADE
C      KARD       CARD OUTPUT KARD=1 NO CARD OUTPUT KARD=0
C      TITLE      TITLE LIMITED TO 80 CARD COLUMNS
C      IBERT      IBERT=1 IF BERTALANFFY GROWTH EQUATION IS USED
C      MAXA       MAXIMUM ARE OF THE SPECIES
C      IBT        MINIMUM AGE AT RECRUITMENT
C      IET        MAXIMUM AGE AT RECRUITMENT
C      XMS        STARTING INST. NATURAL MORTALITY RATE (M)
C      XMI        M INCREMENT
C      NM         NUMBER OF M S TO BE RUN
C      EINC       EXPLOITATION RATE INCREMENT
C      NE         NUMBER OF EXPLOITATION RATES TO BE RUN
C      LINF       BERTALANFFY CONSTANT
C      K          BERTALANFFY CONSTANT
C      TO         BERTALANFFY CONSTANT
C      A          LENGTH-WEIGHT CONSTANT
C      B          LENGTH-WEIGHT CONSTANT
C      PS(I)      PROPORTION SPAWNING BY AGE GROUP
C                 ONLY INPUT FOR AGES IET TO 10 (10+ ARE ASSUMED 1.0)
C
      COMMON M,IBT,IET,EINC,NE,FST(20),FT(20),IS(50,50),IY(50,50)
     1,KARD
      DIMENSION BC(20,50),PS(51),G(51),GH(51),WT(51),WH(51),XL(51),
     1XLH(51),TOT(20),TITLE(20)
      INTEGER T
      REAL M,LINF,K
      READ 399, NRUNS,KARD
  399 FORMAT (2I2)
    1 NRUNS=NRUNS-1
      READ  400,(TITLE(I),I=1,20)
  400 FORMAT(10A8,/,10A8)
      PRINT 401,(TITLE(I),I=1,20)
  401 FORMAT(1H1,//,1X,10A8,/,1X,10A8)
      READ 100,IBERT,MAXA,IBT,IET,XMS,XMI,NM,EINC,NE
  100 FORMAT (4I3,2F5.3,I3,F5.3,I3)
      IF (IBERT.NE.1)  GO TO 2
      READ 101 , LINF,K,TO,A,B
  101 FORMAT(F10.2,F10.6,F15.9,F15.12,F10.6)
      PRINT 102, LINF,K,TO,A,B
  102 FORMAT (T5,*BERTALANFFY CONSTANTS*,/,T8,*L INFINITY =*,F10.2,/,
     1T8,*K =*,F10.6,/,T8,*TO =*,F10.6,//,T5,*LENGTH-WEIGHT CONSTANTS
     2*,/,T8,*A=*,F15.12,/,T8,*B=*,F10.6,/)
      GO TO 4
C     ADD OTHER INPUT OPTION
    2 CONTINUE
      READ 666,(WT(N),N=1,15)
  666 FORMAT (10F6.2)
      READ 668,(PS(N),N=1,10)
  668 FORMAT (10F6.4)
      DO 670 N=11,51
  670 PS(N)=1.0
      DO 671 N=1,14
      TEMP=WT(N+1) / WT(N)
  671 G(N)=GH(N)=TEMP
      DO 672 N=15,MAXA
      GH(N)=G(N)=TEMP
  672 WT(N)=WT(N-1)* TEMP
      IF (IBERT.EQ.0) GO TO 7
      GO TO 38
    4 DO 5 I=1,51
    5 PS(I)=1.0
      READ 103,(PS(I),I=IBT,10)
  103 FORMAT(10F6.4)
      IA=MAXA+1
      DO  6 N=IET,IA
      XL(N) = LINF* (1-EXP(-K*N + K*TO))
      U = N + 0.5
      XLH(N) = LINF* (1-EXP(-K*U + K*TO))
      WT(N) = A*XL(N) **B
      WH(N) = A*XLH(N)**B
      GH(N) = WH(N)/WT(N)
      IF (N.GT.IBT)  G(N-1) = WT(N)/WT(N-1)
    6 CONTINUE
C     NOTE THAT THE UNITS ARE DEPENDENT UPON INPUT
    7 PRINT 200
  200 FORMAT (//,1X,*AGE   LENGTH   WEIGHT        PS       GROW     GROWH*)
      DO 8 N=IBT,MAXA
      PRINT 104,N,XL(N),WT(N),PS(N),G(N),GH(N)
  104 FORMAT (1X,I3,2F9.2,3F9.3)
    8 CONTINUE
      M=XMS-XMI
      DO 26 MM=1,NM
      TCT(MM)=0
      M=M+XMI
      E=-EINC
      DO 24 J=1,NE
      E=E + EINC
      F=E   $   N=0
      IF(E.EQ.0) GO TO 12
   10 N=N+1  $   IF(N.GT.50) GO TO 90
      EV=EVAL(F)
      E1=EVAL(F-0.01)  $  E2=EVAL(F+0.01)
      SLOPE=(E2-E1) /0.02
      DIFFE=EV-E
      F=F-DIFFE/SLOPE
      IF(ABS(DIFFE).GT.0.000001) GO TO 10
   12 FST(J)=F
      Z=M+F
      DO 22 I=IBT,IET
      HS = C = 0
      POP=1000
      DO 20 T=IET,MAXA
      IF(I.GT.IET) GO TO 15
      IF(F.EQ.0) TCT(MM)=TCT(MM)+POP
      IF(F.EQ.0) BC(MM,T)=POP
   15 HS=HS + POP*PS(T)
      IF (T.LT.I)  GO TO 14
      W=Z
      FF=F
      GO TO  16
   14 W=M
      FF=0
   16 C=POP*(1-EXP(-W))
      IF(FF.EQ.0) GO TO 18
      C=D*(FF/Z)*GH(T) + C
   18 POP=(POP-C) * G(T)
   20 CONTINUE
      IS(I,J) = HS
      IY(I,J) = C
   22 CONTINUE
   24 CONTINUE
      PRINT 105,M
```

```
105 FORMAT (//,31X,*YIELD PER METRIC TON OF RECRUITS M=*,F6.4,//,
   1* AGE*,36X,*(IN KG.)*,/,* AT*,/,* REC.*)
    CALL OUTISO(IY)
    PRINT 110,M
110 FORMAT (//,31X,*SPAWNING BIOMASS OVER LIFE OF COHORT M=*,F6.4,
   1//,* AGE*,/,* AT*,/,* REC.*)
    CALL OUTISO(IS)
 26 CONTINUE

    PRINT 111
111 FORMAT (//,31X,*BIOMASS CURVES WITH NO FISHING MORTALITY*//,1X,
   1*AGE          INSTANTANEOUS NATURAL MORTALITY*,//)
    M=XMS-XMI
    DO 28 N=1,NM
    M=M+XMI
 28 FT(N)=M
    PRINT 112,(FT(N),N=1,NM)
112 FORMAT (7X,20F6.2)
    IYR=IBT-1
    DO 30 I=IET,MAXA
    IYR=IYR+1
    PRINT 113,IYR,(BC(MM,I),MM=1,NM)
113 FORMAT (1X,I4,2X,20F6.0)
 30 CONTINUE
    DO 34 MM=1,NM
    DO   32 I=IBT,MAXA
    BC(MM,I)=BC(MM,I)/TOT(MM)
 32 CONTINUE
 34 CONTINUE
    PRINT 115
115 FORMAT(//,31X,*PROPORTION OF THE POPULATION BY WEIGHT F=0*,
   1//,* AGE          INSTANTANEOUS NATURAL MORTALITY*,//)
    PRINT 112,(FT(N),N=1,NM)
    IYR=IBT-1
    DO 36 I=IET,MAXA
    IYR=IYR+1
    PRINT 116,IYR,(BC(MM,I),MM=1,NM)
116 FORMAT(1X,I4,2X,20F6.4)
 36 CONTINUE
    IF(NRUNS.GT.0) GO TO 1
    GO TO 999
 38 PRINT 444
444 FORMAT (//,* OPTION NOT INSTALLED*)
 90 PRINT 998
998 FORMAT(//,*  ITERATIONS FOR F EXCEEDED 50 *)
999 STOP  $ END

    FUNCTION EVAL(F)
    COMMON M   $   REAL M
    EVAL=(1.0-EXP(-F-M)) * F/(F+M)
    RETURN $ END

    SUBROUTINE  OUTISO(JT)
    COMMON M,IBT,IET,EINC,NE,FST(20),FT(20),IS(50,50),IY(50,50)
   1,KARD
    REAL M
    DIMENSION JT(50,50)
    NN=-1
    DO 200 N=IBT,IET
    NN=NN+1
    I=IET-NN
200 PRINT 201,I,(JT(I,J),J=1,NE)
201 FORMAT (//,2X,I2,2X,20I6)
    TEM=-EINC
    DO 202 N=1,NE
    TEM = TEM+EINC
```

```
  202 FT(N) = TEM
      PRINT 203,(FT(N),N=1,NE)
  203 FORMAT(///,* E       *,20F6.3)
      PRINT 204,(FST(N),N=1,NE)
  204 FORMAT(* F       *,20F6.3)
      PRINT 205
  205 FORMAT(/,6X,*E = EXPLOITATION RATE, F = INST. FISHING MORT.RATE*)
      IF(KARD.EQ.0) GO TO 210
      DO 206 I=IBT,IET
  206 PUNCH 207,(JT(I,J),J=1,NE)
  207 FORMAT (10I8,/,10I8)
      PUNCH 208
  208 FORMAT (/)
  210 RETURN  $  END
```

```
   TYPICAL INPUT FOR ISCE


  2                   NUMBER OF RUNS
BOCACCIO ROCKFISH              DATA FROM PHILLIPS(1964) CFG FISH BULL. 126
APRIL 14, 1976     RH PARRISH
  1 30  1 10 .200 .050  3 .020 20
    812.97    .14784         -0.6439  .000000012860    3.0941
000000000000    .1    .5    .8   1.0   1.0   1.0   1.0   1.0
CHILEPEPPER ROCKFISH           DATA FROM PHILLIPS(1964) CFG FISH BULL. 126
APRIL 14, 1976     RH PARRISH
  1 16  1 10 .300 .050  3 .020 20
    552.67    .18204         -0.2283  .000000006260    3.2438
000000   .05    .3    .5    .8   1.0   1.0   1.0   1.0   1.0
```

APPENDIX II. QUOTA SIMULATION PROGRAM.

```
      PROGRAM QUOTAE (INPUT,OUTPUT,PUNCH)

C     QUOTA SIMULATION MODEL    RH PARRISH  JUNE 15,1976

C     CONTROL CARD VARIABLE DESCRIPTIONS

C       ITO      BEGINNING YEAR OF THE SIMULATION
C       NYRS     NUMBER OF YEARS FOR THE SIMULATION
C       IBT      MINIMUM AGE AT RECRUITMENT
C       IET      MAXIMUM AGE AT RECRUITMENT
C       MAXA     MAXIMUM AGE
C       IRUN     CONTROL FOR OUTPUT
C                  IRUN=0  OUTPUT IS LIMITED TO YIELD MATRICES
C                  IRUN=1  OUTPUT IS ANNUAL SPAWNING BIOMASS + YIELD MATRICIES
C                  IRUN=2  OUTPUT IS ANNUAL SPAWNING BIOMASS, YIELD, TOTAL
C                          BIOMASS AND RECRUIT BIOMASS + YIELD MATRICIES
C       ILOGI    ILOGI=0 FOR CONSTANT PS(1)
C                ILOGI=1 FOR DENSITY DEPENDENT PS(1)
C       IENV     IENV= THE NUMBER OF ENVIRONMENTAL VARIABLES INPUT
C                      MAXIMUM NUMBER IS 6, FORMAT IS ON LINE 128
C                IENV=0  IF NO ENVIRONMENTAL VARIABLES ARE INPUT
C       IPRO     IPRO=0, =1, =2  DEPENDING ON THE NO. OF PRORATED
C                  ENVIRONMENTAL VARIABLES, FORMAT IS ON LINES 133,137
C       IQSET    SETS THE BIOMASS SEGMENT THAT THE QUOTA IS BASED ON
C                  IQSET=0  QUOTA BASED ON SPAWNING BIOMASS
C                  IQSET=1  QUOTA BASED ON TOTAL BIOMASS
C                  IQSET=2  QUOTA BASED ON AGE I + AGE II BIOMASS
C       RMAX     MAXIMUM RECRUIT BIOMASS ALLOWED
C       QAL      LOWER QUOTA LEVEL
C       QBL      UPPER QUOTA LEVEL
C       M        INSTANTANEOUS NATURAL MORTALITY RATE
C       SLP      SUBLEGAL PROPORTION (SETS CATCH OF UNDERSIZED FISH)
C       QA       LOWER QUOTA PROPORTION
C       QMIN     MINIMUM UPPER QUOTA PROPORTION
C       QINC     INCREMENT FOR UPPER QUOTA PROPORTION
C       NQ       NUMBER OF QUOTA PROPORTIONS
C       BPOP(N)  BEGINNING BIOMASS BY AGE GROUP
C       PS(N)    PROPORTION SPAWNING BY AGE GROUP
C       G(N)     PROPORTION ANNUAL GROWTH BY AGE GROUP
C       GH(N)    PROPORTION GROWTH FOR HALF OF THE YEAR BY AGE GROUP
C                ( IE AVERAGE GROWTH TO CAPTURE)
      COMMON
     0ITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
     1Q2,QA,QB,QAL,QBL,GPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
     2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ,
     3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
     4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51),
     5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
      REAL M
      INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPOP      ,
      READ 001,KL
  001 FORMAT(I2)
      DO 199 KLM=1,KL
      READ 100,ITO,NYRS,IBT,IET,MAXA,IRUN,ILOGI,IENV,IPRO,IQSET,
     1RMAX,QAL,QBL,M,SLP,QA,QMIN,QINC,NQ
  100 FORMAT (10I4,/,3F8.0,5F4.2,I4)
      IF(KLM.GT.1) GO TO 102
      READ 101,(BPOP(N),PS(N),G(N),GH(N),N=IBT,MAXA)
  101 FORMAT (F6.0,3F6.4)
  102 PRINT 103,M,NYRS,ITO
  103 FORMAT    (*1TWO STEP QUOTA SIMULATION MODEL FOR *,
     1*PACIFIC MACKEREL   RH PARRISH   MAY 18, 1976*
     I,/,* ALL POP FIGURES IN THOUSANDS OF POUNDS*
     3,/,* NATURAL MORTALITY  M=*,F4.2,/,* SIMULATED FOR  *,I4,* YEARS*
     4,/,* STARTING POPULATION *,I4,//,* MODEL PARAMETERS BY AGE GROUP*
     5,/,* AGE      STARTING     PRCPORTION     PROPORTION       PROPORTION
     6GROWTH*,/,* GROUP   POPULATICN     SPAWNING     ANNUAL GRCWTH       T
     7O CAPTURE*)
      PRINT 104,(N,BPOP(N),PS(N),G(N),GH(N),N=IBT,MAXA)
  104 FORMAT(I2,F13.0,F12.3,F15.3,F18.3)
  105 FORMAT(//,60H EXTINCTION CURVE FOR PS(1)=0.54*EXP(-.0000071709*TPO
     1P)       )
      IF (ILOGI.EQ.1) PRINT 105
      IF(IQSET-1)106,108,110
  106 PRINT 107
  107 FORMAT(//,* QUOTA BASED ON SPAWNING BIOMASS*)
      GO TO 112
  108 PRINT 109
  109 FORMAT(//,* QUOTA BASED ON TOTAL BIOMASS*)
      GO TO 112
  110 PRINT 111
  111 FORMAT(//,* QUOTA BASED ON THE BIOMASS OF AGEI + AGEII*)
  112 PRINT 113,QAL,QA,QBL
  113 FORMAT (//,* LCWER QUOTA LEVEL =*,F8.0,/,* LOWER QUOTA PROPORTICN=
     1*,F6.3,/,* UPPER QUOTA LEVEL = *,F8.0)
      PRINT 114
  114 FORMAT (//,* RECRUITMENT MODEL*,//,1X,
     1* RICKER BMOP3R TRANSPORT MODEL*,/,
      PRINT 115,IBT,IET,IRUN,ILCGI,IENV,IPRO,IQSET,RMAX,SLP,MAXA,QMIN,
     1QINC,NQ
  115 FORMAT(//,* IBT=*,I4,/,* IET=*,I4,/,* IRUN=*,I4,/,* ILOGI=*,I4,/,
     1* IENV=*,I4,/,* IPRO=*,I4,/,* IQSET=*,I4,/,* RMAX=*,F8.0,/,
     2* SLP=*,F4.2,/,* MAXA=*,I4,/,* QMIN=*,F5.3,/,* QINC=*,F5.3,/,
     3* NQ=*,I4)
      IF(KLM.GT.1) GO TO 119
      IF(IENV.GT.0) GO TO 150
      IF(IPRO.GT.0) GO TO 150
  116 CONTINUE

C     BODY STARTS HERE
  119 IF(NQ.EQ.1) GO TO 120
      GO TO 122
  120 IU=-9
      DO 121 N=IBT,IET
  121 CALL MACQE
      CALL OUTM
      STOP
  122 IU=NQ  $  QB=QMIN-QINC  $  NL=IET-IBT+1
      DO 124 IQB=1,NQ
      QB=QB+QINC  $  L=0
      DO 123 J=IBT,IET
      L=L+1
      CALL MACQE
      MAT(L,IQB)=TYIELD(L)/NYRS
  123 MA(L,IQB)=ACATCH
  124 CALL OUTM
      PRINT 125,NYRS
  125 FORMAT (1H1,//,20X,I4,* YEAR MEAN YIELD*)
      CALL OUTMAT(MAT)
      IT=IT0+NYRS-1
      PRINT 126,IT
  126 FORMAT (1H1,//,20X,*YIELD IN *,I4)
      CALL OUTMAT(MA)
      GO TO 199
  150 IF(IENV.LT.1) GO TO 160
      DO 151 N=1,NYRS
  151 READ 152,(ENV(N,NN),NN=1,IENV)
  152 FORMAT(6F8.2)
```

```
160 IF(IPRO.GT.0) GO TO 161
    GO TO 116
161 DO 162 N=1,NYRS
162 READ 163, (ENV(N,NN),NN=7,9)
163 FORMAT(35X,3F5.0)
    IF(IPRO.EQ.1) GO TO 116
    DO 164 N=1,NYRS
164 READ 165, (ENV(N,NN),NN=10,12)
165 FORMAT(35X,3F5.0)
    GO TO 116
199 CONTINUE
    STOP  $  END

    SUBROUTINE MACGE
    COMMON
   0IIO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),[illegible]
   1Q2,QA,QB,QAL,QBL,GPOP,SUBC,CC,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
   2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NC,
   3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
   4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51),
   5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
    REAL M
    INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPOP
    TSPOP(L) =TREC(L)=TYIELD(L)= TTPOP(L)=0
    DO 500 N=IBT,MAXA
500 POPA(N)=BPOP(N)
    DO 516 I=1,NYRS
    SPOP=ACATCH=TPOP=0
    DO 501 N=IBT,MAXA
    POPC(N)=POPA(N)*GH(N)
501 TPOP=TPOP+POPA(N)
    IF(ILOGI.EQ.1) CALL LOGI
    DO 502 N=IBT,MAXA
502 SPOP=SPOP+POPA(N)*PS(N)
    CALL FUN
    IF (IQSET-1)503,504,505
503 Q2=SPOP  $  GO TO 506
504 Q2=TPOP  $GO TO 506
505 Q2=POPA(1)+POPA(2)
506 IF(Q2.LT.CAL) GO TO 507
    GO TO 508
507 Z=M  $  A=1.0-EXP(-Z)
    DO 58 N=IBT,MAXA
 58 XMORT(N) = POPA(N)*A
    GO TO 512
508 CALL QUOT
    E=CQ/QPOP
    F=FVAL(E,M)
    Z=F+M  $  A=1.0 -EXP(-7)
    DO 509 N=J,MAXA
    XMORT(N) = POPA(N)*A
509 ACATCH = ACATCH + XMORT(N)*(F/Z)*GH(N)
    IF(J.GT.IBT)  GO TO 510
    GO TO 512
510 E = SUBQ/SUBPOP
    F=FVAL(E,M)
    ZS=F +M   $  AS=1.0 - EXP(-ZS)
    JT=J-1
    DO 511 N=IBT,JT
    XMORT(N) = POPA(N)*AS
511 ACATCH=ACATCH + XMORT(N) * (F/ZS) * GH(N)
512 NT=MAXA+2
    DO 513 N=IBT,MAXA
    NT=NT-1
```

```
  513 POPA(NT)=(POPA(NT-1)-XMORT(NT-1)) * G(NT-1)
      POPA(MAXA) = POPA(MAXA) + POPA(MAXA+1)
      POPA(IBT)=REC
      TSPOP(L)=TSPOP(L) + SPOP
      TREC(L) = TREC(L) + REC
      TYIELD(L) = TYIELD(L) + ACATCH
      TTPOP(L) = TTPOP(L) + TPOP
      ASPOP(I,L) = SPOP
      AREC(I,L) = REC
      AYIELD(I,L) = ACATCH
      ATPOP(I,L) = TPOP
      IF(REC.GT.RMAX)  GO TO 514
      GO TO 516
  514 PRINT 515
  515 FORMAT (* RECRUITMENT BLEWUP OR FAILED*)
      CALL OUTM
      STOP
  516 CONTINUE
  517 RETURN  $  END

      SUBROUTINE  FUN
      COMMON
     0ITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
     1Q2,QA,QB,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
     2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ,
     3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL
      REAL M
      IF(IPRO.EQ.0)  GO TO 666
      P(1)=(PS(1)*POPA(1)) /SPOP
      P(2)=(PS(2)*POPA(2))/SPOP
      P(3)=(PS(3)*POPA(3) +POPA(4) +POPA(5) +POPA(6))/SPOP
      PROA=P(3)*ENV(I,7)+P(2)*ENV(I,8) + P(1)*ENV(I,9)
      IF(IPRO.EQ.2) PROB=P(3)*ENV(I,10)+P(2)*ENV(I,11)+P(1)*ENV(I,12)
  666 CONTINUE
C     RECRUITMENT MODEL AFTER THIS CARD
     2* REC= 0.97815*SPOP*EXP(-0.00037741*SPOP)*EXP(0.020787*PROA)
     3 *EXP(0.0039065*PROB)  *)
      RETURN  $  END

      FUNCTION FVAL(E,M)
C     ITERATIVE SOLUTION FOR INST. FISHING MORT. GIVEN EXPLOITATION RATE
C     AND INST. NATURAL MORT.
      COMMON ITO, NYRS
      REAL M
      F=E  $  N=0
      IF(E.EQ.0) GO TO 2
    1 N=N+1  $  IF(N.GT.50) GO TO 90
      F1=F-0.01   $   F2=F+0.01
      EV=(1.0 - EXP(-F-M))* F/ (F+M)
      E1=(1.0 - EXP(-F1-M))* F1/ (F1+M)
      E2=(1.0 - EXP(-F2-M))* F2/ (F2+M)
      SLOPE= (E2-E1) / 0.02
      DIFFE = EV-E
      F=F - DIFFE / SLOPE
      IF(ABS(DIFFE).GT.0.000001) GO TO 1
    2 FVAL=F
      RETURN
   90 PRINT 900
  900 FORMAT(//,*  ITERATIONS FOR F EXCEEDED 50*)
  901 STOP  $  END

      SUBROUTINE LOGI
C     PACIFIC MACKEREL SUBROUTINE
      COMMON
     0ITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12)
      PS(1)=.54*EXP(-.0000071709*TPOP)
      RETURN $ END
      SUBROUTINE QUOT
      COMMON
     0ITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
     1Q2,QA,QB,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
     2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ,
     3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL
      REAL M
      IF(Q2.GT.QBL) GO TO 900
      QUO=QA*(Q2-QAL)
      GO TO 901
  900 QUO=(QBL-QAL)*QA + (Q2-QBL)*QB
  901 QPOP=SUBQ=0.01  $  SUBPOP=0.1
      DO 902 IC=J,MAXA
  902 QPOP=QPOP+POPC(IC)
      IF(J.EQ.IBT) GC TO 904
      JJ=J-1
      DO 903 IC=1,JJ
  903 SUBPOP=SUBPOP + POPC(IC)
      SUBQ=SLP*QUO
      QUO=QUO-SUBQ
      IF(QUO/QPOP.GT.1.0) GO TO 905
  904 CQ=QUO  $  GO TO 906
  905 CQ=QPOP
  906 IF(SUBQ/SUBPOP.LT.0.5) GO TO 907
      X=0.5*SUBPOP  $  Y=SUBQ-X
      SUBQ=X   $   CG=QUO+Y
  907 RETURN   $  END

      SUBROUTINE OUTM
      COMMON
     0ITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
     1Q2,QA,QB,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
     2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ,
     3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
     4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51),
     5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
      REAL M
      INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIFLD,TREC,TTPOP
      IF(REC.GT.RMAX) GO TO 606
      IF(IRUN.EQ.0) GO TO 609
      IOK=1
      IF(QBL.LT.1.AND.IQSET.EQ.1) IOK=0
      IF(IOK.EQ.1) PRINT 600,QB
      IF(IOK.NE.1) PRINT 601,QB
  600 FORMAT(//,T21,*ANNUAL SPAWNING BIOMASS, UPPER QUOTA PROPORTION =*
     1,F6.3)
  601 FORMAT(//,T21,*ANNUAL SPAWNING BIOMASS, EXPLOITATION RATE =*,F6.3)
      CALL OUTP (ASPOP,TSPOP)
      IF(IRUN.EQ.1) GO TO 609
      IF(IOK.EQ.1) PRINT 602,QB
      IF(IOK.NE.1) PRINT 603,QB
  602 FORMAT (//,T21,*ANNUAL YIELD, UPPER QUOTA PROPORTION =*,F6.3)
  603 FORMAT (//,T21,*ANNUAL YIELD, EXPLOITATION RATE =*,F6.3)
      CALL OUTP (AYIELD,TYIELD)
      IF(IOK.EQ.1) PRINT 604,QB
      IF(IOK.NE.1) PRINT 605,QB
  604 FORMAT (//,T21,*ANNUAL TOTAL BIOMASS, UPPER QUOTA PROPORTION =*
     1,F6.3)
  605 FORMAT (//,T21,*ANNUAL TOTAL BIOMASS, EXPLOITATION RATE =*,F6.3)
      CALL OUTP (ATPOP,TTPOP)
  606 CONTINUE
      IF(IOK.EQ.1) PRINT 607,QB
      IF(IOK.NE.1) PRINT 608,QB
  607 FORMAT (//,T21,*ANNUAL RECRUITMENT, UPPER QUOTA PROPORTION =*
     1,F6.3)
```

```
608 FORMAT (//,T21,*ANNUAL RECRUITMENT, EXPLOITATION RATE =*,F6.3)
    CALL OUTP (AREC,TREC)
609 RETURN  $  END

    SUBROUTINE OUTP (IANN,ITOT)
    COMMON
   0ITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
   1Q2,QA,QB,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
   2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ,
   3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
   4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51),
   5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
    REAL M
    INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPOP
    DIMENSION IANN(100,16),ITOT(100)
    PRINT 700,(N,N=IBT,IET)
700 FORMAT(///,T21,*AGE AT RECRUITMENT*,//,* SEASON*,16I8)
    IS=ITO-1
    DO 701 N=1,NYRS
    IS=IS+1
701 PRINT 702,IS,(IANN(N,K),K=1,NL)
702 FORMAT (1X,I4,2X,16I8)
    IF(IU.NE.-9) RETURN
    DO 703 N=IBT,IET
703 ITOT(N) = ITOT(N)/NYRS
    PRINT 704,(ITOT(N),N=IBT,IET)
704 FORMAT (*  MEAN *,16I8)
    RETURN  $  END

    SUBROUTINE OUTMAT(MT)
    COMMON
   0ITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
   1Q2,QA,QB,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
   2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ,
   3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
   4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51),
   5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
    REAL M
    INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPOP
    DIMENSION MT(16,16)    ,QQ(16)
    PRINT 800
800 FORMAT (* AGE*,/,*  AT*,/,* REC.*)
    K=IET+1
    DO 801 NJ=1,NL
    K=K-1
C   PUNCH CARD OUTPUT FOR YIELD ISOPLETH PLOTS
    PUNCH 008,(MT(K,N),N=1,NQ)
008 FORMAT (10I8)
801 PRINT 802 ,K,(MT(K,N),N=1,NQ)
802 FORMAT (//,1X,I2,4X,16I8)
    PRINT 803
803 FORMAT (//,7X)
    QY=QMIN-QINC
    DO 804 N=1,NQ
    QY=QY+QINC
804 QQ(N)=QY
    PRINT 805,(QQ(N),N=1,NQ)
805 FORMAT (7X,16F8.2)
    IF(IQSET.NE.1) GO TO 807
    IF(QBL.LT.1.0) PRINT 806
806 FORMAT(/,T32,*EXPLOITATION RATE*)
    IF(QBL.LT.1.0) GO TO 899
807 PRINT 808
808 FORMAT(/,T32,*QUOTA PROPORTION*)
899 RETURN  $  END
```

```
      TYPICAL INPUT FOR QUOTAE


  4                         NUMBER OF RUNS
 1946   30    1    5    6    2    1    0    2    0
  900000.  20000.  40000. .50 .10 .20 .00 .05  10
  18933 .00   1.549 1.316
  51286 .77   1.508 1.207
  30137 .88   1.282 1.143
  143011.00   1.2   1.103
  167831.00   1.146 1.076
      01.00   1.109 1.057
 30N 119W 1946              110   80  132  155  252  347  207  201  207   86   54   53
 30N 119W 1947              110   60  111  191  114  176  243  152  102   95   79   61
 30N 119W 1948               50  102   82   61  220  151  126  119  105   81   72   31
 30N 119W 1949               63  121   90  150  158  160  113  155  123   91   84   53
 30N 119W 1950               60   59  117  151  153  164   76  121  101   70   58   88
 30N 119W 1951              112   85  115   91  204  207  157  120  155  128   73   49
 30N 119W 1952               24   35  108   99  224  156   84  115   98  107   54   31
 30N 119W 1953               56  125  158  183  218  235  143  191  154  139  128  113
 30N 119W 1954               77   94   77  174  173  210  108  178  164  105   69   49
 30N 119W 1955               81   68   99  226  265  299  202  173  242  173  111   61
 30N 119W 1956               72   98  207  165  238  297  191  245  180  139   60   52
 30N 119W 1957               20   56  165  184  190  274  202  170  167  122   93   71
 30N 119W 1958              105   75  101  229  191  258  185  130  165  130  115   57
 30N 119W 1959               99   33  168  149  231  304  195  139  151  153   64   27
 30N 119W 1960               45  100  169  144  299  133  111  138  133  121   47   66
 30N 119W 1961               33  157  168  164  210  158   94  124   70   66   47   53
 30N 119W 1962               49   46   82  189  212  218  155  166  148   97  103   32
 30N 119W 1963                9   63   87  115  150  163  182  131   93   71   63   41
 30N 119W 1964               69   63  149  169  225  204  176  134  118   60   38   73
 30N 119W 1965               44   54   50   39  185  142   95   74   59   58    1   27
 30N 119W 1966               44   49   72   64   81  121  132   61   76   51   14   42
 30N 119W 1967               29   65   56   73  163  130  126  156   71   91   13   58
 30N 119W 1968               32   30   92  116  152  157  102  108  104   76   90   32
 30N 119W 1969                8   45  136  185  227  194  219  202  173  134    7   70
 30N 119W 1970               27   13   96  183  241  238  177  225  158  117   55   45
 30N 119W 1971               82  164  160  232  241  265  196  147  170  142  139   82
 30N 119W 1972               91   88  186  180  165  168  125  113   90   61   67   85
 30N 119W 1973               64    7  178  192  155  178  137  149  121   90   93   97
 30N 119W 1974               22  104   93  234  284  263  147  167  141  104   74   34
 30N 119W 1975               50   62  127  174  187  197  192  194  180  146  134   58
 30N 119W 1946 ODI          467   30   68 -201 -658 -578 -254  -69  -51  -51   88   34
 30N 119W 1947 ODI          -78   48 -114 -140 -362 -303 -107 -274 -124  -46  237  104
 30N 119W 1948 ODI          -75   68  -55 -270 -322 -338 -117 -107  -75   93  215   26
 30N 119W 1949 ODI          102  125 -188 -167 -309 -105 -137  -56   50   78  184   87
 30N 119W 1950 ODI          -76  -78   54 -206 -346 -356  -52 -120 -247 -141    3  -26
 30N 119W 1951 ODI         -113  -36   84 -211 -449 -374 -162 -169 -266   12   -4   66
 30N 119W 1952 ODI          -20  -68  -42  -55 -330 -278 -342 -134 -221 -152  -57  -17
 30N 119W 1953 ODI           63  246 -255 -441 -439 -695 -362 -594 -532 -284 -121  166
 30N 119W 1954 ODI          -31  -68 -166 -492 -455 -459 -195 -528 -118 -229   47  -75
 30N 119W 1955 ODI           21  -36 -116 -370 -570 -657 -276 -119 -199 -230  108  -81
 30N 119W 1956 ODI           23  -62  -26 -324 -532 -424 -402 -371 -137 -146  170  110
 30N 119W 1957 ODI          -26 -181 -205 -393 -468 -363 -273 -265 -448 -213  -51  -19
 30N 119W 1958 ODI         -123 -294 -397 -311 -834 -865 -608 -364 -183  -51   19   57
 30N 119W 1959 ODI           -6  -83 -100 -405 -656 -671 -418 -407 -279  -38   57   61
 30N 119W 1960 ODI          -54 -141 -245 -120 -409 -386 -230 -196  -57   -1   -4   76
 30N 119W 1961 ODI           54  -59 -248 -112 -742 -652 -285   33  -40   58   -4  165
 30N 119W 1962 ODI          173  -96 -125 -183 -592 -284 -786 -563 -308 -293  -88   13
 30N 119W 1963 ODI          -20 -121 -336 -524 -619 -814 -875 -524   94    5   46   79
 30N 119W 1964 ODI          102   36 -246 -818-1960-2005-1432-1165 -885 -483 -218 -468
 30N 119W 1965 ODI         -251 -248 -412  -91 -421 -689 -817 -562 -481 -307  -66  -56
 30N 119W 1966 ODI           23 -127 -255 -458 -798-1053 -776 -568 -662 -301 -209 -127
 30N 119W 1967 ODI         -100  -99 -539 -608-1113-1255-1002 -870 -712 -462 -148  145
 30N 119W 1968 ODI         -161 -223 -399 -473-1180-1082 -677 -778 -643 -540 -269  -86
 30N 119W 1969 ODI         -117 -363 -540 -657-1044-1071 -954 -821 -848 -711 -143 -240
 30N 119W 1970 ODI         -197 -168 -357 -513 -801 -810 -561 -680 -429 -457 -249 -165
 30N 119W 1971 ODI           43   20 -374 -471 -549 -859 -800 -422 -544  -63 -206 -125
 30N 119W 1972 ODI           97 -326 -434 -627 -651 -801 -687 -458 -408 -154   96   76
 30N 119W 1973 ODI           -6  -23 -299 -461 -892 -924 -770 -652 -726 -338 -359   63
 30N 119W 1974 ODI          -22   18 -338 -591 -969 -903 -590 -907 -555 -385    3  151
 30N 119W 1975 ODI          189 -204 -332 -503 -909-1223 -741 -832 -535 -379   46   71
 1946   30    1    5    6    2    1    0    2    0
  900000.  20000.  40000. .50 .10 .20 .50 .05  10
 1946   30    1    5    6    2    1    0    2    0
  900000.      0.       0. .50 .10 .20 .50 .05  10
 1946   30    1    5    6    2    1    0    2    0
  900000.      0.       0. .50 .10 .20 .00 .05  10
```

APPENDIX III. UPDATE FOR CDC VERSION OF BMDP3R NONLINEAR REGRESSION.

```
*ID MAY25
*D P3RJUL.2
*I BMDP3R.25
     XMAY 25, 1976 PEG
*D BMDP3R.34
*I BMDP3R.33
      CTOL=1.0E-8
*D UNCOLA.73
*I UNCOLA.72
     X 50H   TOLERANCE FOR CONVERGENCE                      ,F11.8/
*D P3RJUL.24
*I P3RJUL.23
     1      F20.5)
*D RITEIT.15
*I RITEIT.14
 3000 FORMAT(2X,I4,7X,I4,F21.6,1X,F18.7,5(1X,F14.9))
*D REDEV.18
*I REDEV.17
 3600 FORMAT(1X,I4,2X,A1,A8,1X,F14.6,1X,F14.6,2(2X,F13.6))
*D RITEND.28
*I RITEND.27
  900 FORMAT(2X,I4,7X,I4,F21.6,4X,6(1X,F14.6))
*D RITEND.48,RITEND.53
*I RITEND.47
 5600 FORMAT(1H0,2X,7H CASE  ,10HPREDICTED ,7X,
     *  10HSTD DEV OF,5X,8HOBSERVED/
     *  10X,A8,9X,10HPRED VALUE,
     *  5X,A8,9X,A8,4(7X,A8))
 5800 FORMAT(1X,I4,A2,F13.6,2X,F15.5,2X,F13.6,
     *   2X,F15.6,4(2X,F13.6))
*I RITEND.96
      IF(ISFUN.GT.5) GO TO 47
*D FUN.10
*I FUN.9
      IF(ISFUN.GE.1.AND.ISFUN.LE.19)GO TO (100,200,300,400,500,600,700,
     *800,900,1000,1100,1200,1300,1400,1500,1600,1700,1800,1900),ISFUN
*I FUN.99
C
C     RICKER MODEL
  600 F=P(1)*X(1)*EXP(P(2)*X(1))
      DF(1)=X(1)*EXP(P(2)*X(1))
      DF(2)=P(1)*X(1)*X(1)*EXP(P(2)*X(1))
      RETURN
C
C     CUSHING MODEL
  700 F=P(1)*X(1)**P(2)
      DF(1)=X(1)**P(2)
      DF(2)=P(1)*X(1)**P(2)*ALOG(X(1))
      RETURN
C
C     CLARK-RICKER MODEL
  800 F=P(1)*X(1)*EXP(P(2)*X(1))*EXP(P(3)/X(1))
      DF(1)=X(1)*EXP(P(2)*X(1))*EXP(P(3)/X(1))
      DF(2)=P(1)*X(1)*X(1)*EXP(P(2)*X(1))*EXP(P(3)/X(1))
      DF(3)=P(1)*X(1)*EXP(P(2)*X(1)) *(1/X(1)) * EXP(P(3)/X(1) )
      RETURN
C
C     CLARK-CUSHING MODEL
  900 F=P(1)*X(1)**P(2)*EXP(P(3)/X(1))
      DF(1)=X(1)**P(2)*EXP(P(3)/X(1))
      DF(2)=P(1)*X(1)**P(2)*ALOG(X(1))*EXP(P(3)/X(1))
      DF(3)=P(1)*X(1)**P(2) *(1/X(1)) * EXP(P(3)/X(1))
      RETURN
```

```
C
C        CUSHING TRANSPORT MOCEL
 1000 F=P(1)*X(1)**P(2)*EXP(P(3)*X(2))*EXP(P(4)*X(3))
      DF(1)=X(1)**P(2)*EXP(P(3)*X(2))*EXP(P(4)*X(3))
      DF(2)= P(1)*X(1)**P(2)*ALCG(X(1)) *EXP(P(3)*X(2)) *EXF(P(4)*X(3))
      DF(3)= P(1)*X(1)**P(2) *X(2)*EXP(P(3)*X(2)) *EXP(P(4)*X(3))
      DF(4)=P(1)*X(1)**P(2)*EXP(P(3)*X(2))*X(3)*EXP(P(4)*X(3))
      RETURN
C
C       CUSHING SEA LEVEL MCOEL
 1100 F= P(1)*X(1)**P(2) * EXP( P(3)*X(2) )
     1   *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
      DF(1) = X(1)**P(2) * EXP( P(3)*X(2) )
     1   *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
      DF(2) = P(1)*X(1)**P(2)*ALOG(X(1)) * EXP( P(3)*X(2) )
     1   *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
      DF(3) = P(1)*X(1)**P(2) * X(2)*EXP( P(3)*X(2) )
     1   *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
      DF(4) = P(1)*X(1)**P(2) * EXP( P(3)*X(2) )
     1  *X(3)*EXP( P(4)*X(3) ) * EXP( P(5)*X(4) )
      DF(5) = P(1)*X(1)**P(2) * EXP( P(3)*X(2) )
     1   *EXP( P(4)*X(3) ) * X(4)*EXP( P(5)*X(4) )
      RETURN
C
C       EXPONENTIAL MOCEL
C
 1200 F = P(1) * EXP( P(2)*X(1))
      DF(1) = EXP( P(2)*X(1) )
      DF(2) = P(1) * X(1) * EXP(P(2)*X(1))
      RETURN
C
C     RECRUIT PER SPAWNER TRANSPORT MODEL
C
 1300 F = P(1) * EXP(P(2)*X(1)) * EXP(P(3)*X(2)) * EXF(P(4)*X(3))
      DF(1) =     EXP(P(2)*X(1)) * EXP(P(3)*X(2)) * EXF(P(4)*X(3))
      DF(2) = P(1)*X(1)*EXP(P(2)*X(1)) *EXP(P(3)*X(2)) *EXP(P(4)*X(3))
      DF(3) = P(1)*EXP(P(2)*X(1)) *X(2)*EXP(P(3)*X(2)) *EXP(P(4)*X(3))
      DF(4) = P(1)*EXP(P(2)*X(1)) *EXP(P(3)*X(2)) * X(3)*EXP(P(4)*X(3))
      RETURN
C
C       RICKER TRANSPORT MODEL
C
 1400 F  =  P(1)*X(1)*EXP(P(2)*X(1))
     1 * EXP(P(3)*X(2))  *  EXP(P(4)*X(3))
      DF(1) = X(1) * EXP(P(2)*X(1))
     1 * EXP(P(3)*X(2))  *  EXP(P(4)*X(3))
      DF(2) = P(1) * X(1) * X(1) * EXP(P(2)*X(1))
     1 * EXP(P(3)*X(2))  *  EXP(P(4)*X(3))
      DF(3) = P(1) * X(1) * EXP(P(2)*X(1)) * X(2)
     1 * EXP(P(3)*X(2))  *  EXP(P(4)*X(3))
      DF(4) = P(1) * X(1) * EXP(P(2)*X(1)) * X(3)
     1 * EXP(P(3)*X(2))  *  EXP(P(4)*X(3))
      RETURN
C
C       RICKER SEA LEVEL MODEL
C
 1500 F = P(1) * X(1) * EXP(P(2)*X(1))
     1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      DF(1) =    X(1) * EXP(P(2)*X(1))
     1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      DF(2) = P(1) * X(1) * EXP(P(2)*X(1)) * X(1)
     1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      DF(3) = P(1) * X(1) * EXP(P(2)*X(1)) * X(2)
     1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      DF(4) = P(1) * X(1) * EXP(P(2)*X(1)) * X(3)
     1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      DF(5) = P(1) * X(1) * EXP(P(2)*X(1)) * X(4)
     1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      RETURN
```

```
C
C      CLARK-RICKER TRANSPORT MODEL
C
 1600 F=P(1)*X(1)       *EXP(P(2)*X(1)) * EXP(P(3)/X(1))
     1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
      DF(1)= X(1)       *EXP(P(2)*X(1)) * EXP(P(3)/X(1))
     1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
      DF(2)= P(1)*X(1)*X(1) * EXP(P(2)*X(1)) * EXP(P(3)/X(1))
     1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
      DF(3)=P(1)*X(1)*EXP(P(2)*X(1)) * (1.0/X(1)) * EXP(P(3)/X(1))
     1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
      DF(4)=P(1)*X(1) * EXP(P(2)*X(1)) * EXP(P(3)/X(1))
     1*X(2)  * EXP(P(4)*X(2)) * EXP(P(5)*X(3))
      DF(5)=P(1)*X(1) * EXP(P(2)*X(1)) * EXP(P(3)/X(1))
     1* EXP(P(4)*X(2)) * X(3) * EXP(P(5)*X(3))
      RETURN
C
 1700 RETURN
 1800 RETURN
 1900 RETURN
```

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BIOLOGICAL EFFECTS OF OCEAN VARIABILITY: TIME AND SPACE SCALES OF BIOLOGICAL RESPONSE

Paul E. Smith

National Oceanic and Atmospheric Administration, National Marine Fisheries Service,
Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038, U.S.A.

Present biological sampling activities are heavily biassed toward time and space scales of convenience to man, ships and existing equipment rather than to the time and space scales of important events and the biological response to them. Fish populations are observed to undergo sustained increases and decreases for several decades without a commercial fishery. In the first year of life, a California coastal fish may depend on food concentrations less than a metre in extent and be fed upon appreciably by an immature migratory predator (the albacore) spawned 10000 km away. Two multi-million ton fish populations which co-existed in 1940 simultaneously declined in that decade and the unfished anchovy recovered while the sardine did not. The apparently niche-mediated replacement took approximately 10 years, or more than twice the generation time of either species. Since both species are pelagic schooling fish, "competition" is likely to be based on events at the level of the school rather than the individual. These observations, while haphazard in time and space scales, lead to the conclusion that the causes of "unexpected" changes in commercial fish populations should be sought systematically in time and space.

INTRODUCTION

To become more precise, fishery management will require what is not now generally available to it: a suite of carefully timed and spaced measurements of the biological properties contributing to the success or failure of the reproductive process in the open ocean. Vast savings and new insight may be possible by merging physical and chemical oceanography and meteorology with biological oceanography so that critical fishery predictions can be formulated and tested. The main constraint to such a multi-disciplinary approach appears to be the difficulty of obtaining properly timed and spaced data series of sufficient length. It is the purpose of this paper to relate some examples of time and space scales of biological response to ocean variability which are only yet dimly perceived.

THE DECLINE OF THE NORTHERN SUB-POPULATION OF THE PACIFIC SARDINE

After the development of a fishery which peaked at 700000 tons in the 1936–1937 season (Fig. 98), it appears that the spawning biomass of the northern sub-population of the Pacific sardine declined from 4 million metric tons in the early 1930's to less than 10 thousand metric tons by 1965. This 400-fold drop in 30 years was undoubtedly influenced in its later stages by a continued intensive fishery on the small remaining fraction of the stock. It appears that the direct effects of the fishery were augmented by two indirect population effects and their environmental root causes.

The first indirect effect of the fishery was to reduce the number of effective spawning year classes from ten to two. It now appears that two successive failures in reproductive success dramatically lowered the population and this was followed by increased fishing mortality rates. The smaller number of reproducing year classes had sensitized the population to shorter and more frequent survival anomalies (Murphy, 1966). The second indirect effect of the fishery was that the reproductive portion of the stock, being smaller than in the virgin stock, progressively ranged over far smaller areas. This spatial equivalent of the temporal sensitivity induced by the fishery may have made the sardine stock sensitive to reproduction failures over a much smaller geographic region.

In what stage did these survival anomalies take place? If the years 1952 to 1956 are representative, survival variation increased rather steadily from the short embryonic and larval stages through the period when the fish entered the fishery at two years of age. The winter productivity minimum may have accelerated the process somewhat (Fig. 99).

In what area did these survival anomalies take

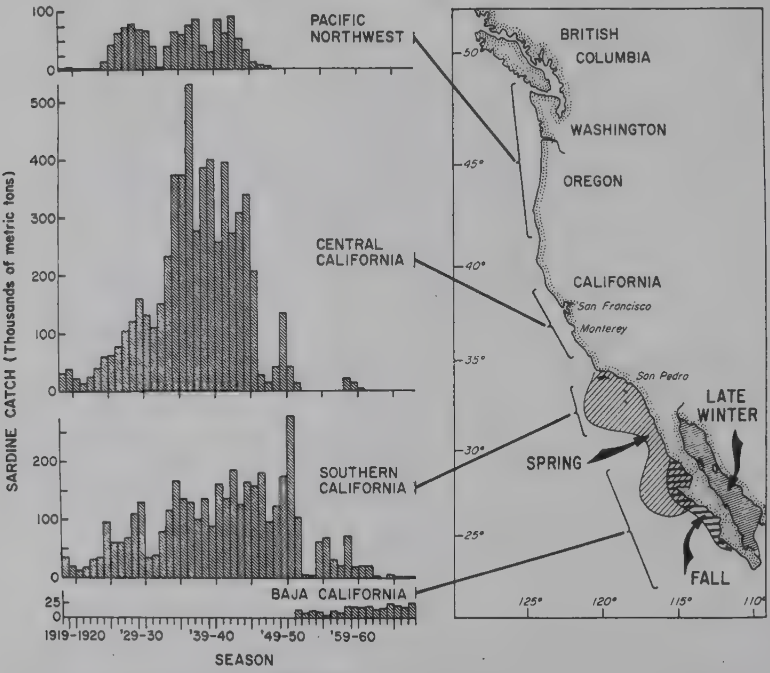

Figure 98. Time series of seasonal catch of Pacific sardine by region (Table 1, p. 184–185, Ahlstrom and Radovich, 1970) of catch compared with the spawning regions and seasons (Marr, 1960).

place? (Fig. 100). In the virgin stock, it would appear that following spawning, the adults would migrate northward to the productive upwelling areas off northern California, Oregon, Washington and British Columbia. Following the autumnal decline in the zooplankton standing stock (Fig. 101), the adults returned to the spawning grounds in the south off Mexico and the southern half of California. Fat stored as a result of feeding along the entire 1500 miles of upwelling coastline was used by the fish to elaborate egg yolk in the southern 500 miles. It appears from subsequent time series of zooplankton volume and temperature distribution that the boundary of low plankton volume in the south and the boundary of low temperature in the north shifted north and south along the coast. These boundaries may also have approached each other, restricting the geographic range of the sardine spawning, or separated broadening the geographic range of the sardine. The virgin stock spawned over the entire area and the annual position of an optimum survival area would be occupied by the population each year. With the reduction of the adult population by the fishery, the stock was unable to occupy the whole area and the optimum site for survival might not coincide with the location of the reduced population.

Beyond these unsatisfying generalizations, little information can now be assembled in retrospect. It may be that as the results of overfishing progress from inconvenience to economic failure, to possible human disaster, we will need to expend more resources on exploratory research systematically along time scales and space scales specifically designed to determine the causes of "unexpected changes" in reproductive success of fish populations.

TIME SCALES

On the short time scale of days–weeks, upwelling, advection and mixing may be observed to be unfavourable for clupeid brood areas (Lasker, 1975). Indeed, the spawning of sardine and anchovy appears

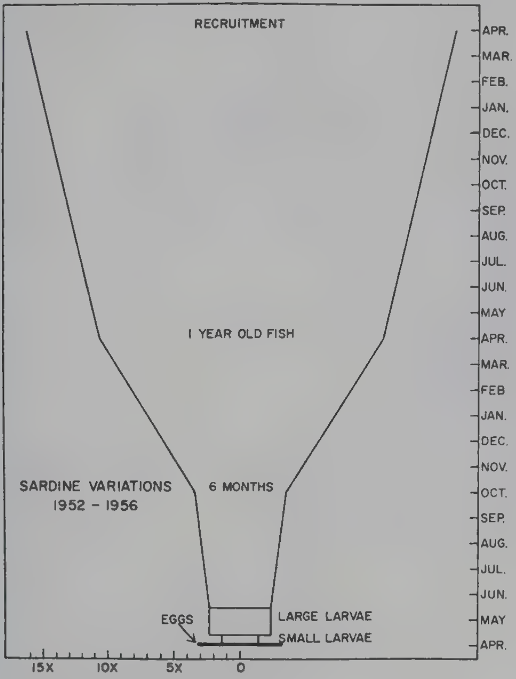

Figure 99. Time course and amplitude of annual variation in the numbers of sardine eggs, larvae, juveniles and pre-recruits from 1952 through 1956.

to occur principally in the stable periods and areas of the western coast of North America rather than the areas of maximum upwelling, mixing and advection, though such areas may be optimal later on for the juvenile states. It is likely that the analysis of these short-term events, in the context of the spring bloom and the spawning and survival of the commercial fishes will require observation each two weeks for several months at the beginning of each year off California. Analysis of survival in other areas may require similar intense and precisely timed observations.

On an annual time scale, juvenile Pacific sardine and northern anchovy must compete with the standing stock of the adults of its own species and to varying degrees with the adults of other species having similar requirements. It appears likely that food, and particularly the location of the remaining food, becomes critical in the winter when primary and secondary production are apparently relatively low and the standing crop of net zooplankton is decreasing. Furthermore, the juveniles contain little fat, and are usually located not far from the spawning grounds during the winter period when the adults return from feeding migrations of the preceding few months. While the individual juveniles are lighter in weight, their tremendous numbers make their total weight, and therefore their food requirements, often larger than the next most abundant, and one year older year class. The winter confrontation between the 0-group juveniles and older fishes is a period which requires special study.

The decadal time scale offers one of the great puzzles of fishery population work. One would expect from theory and from examination of the annual controls on survival that there would be a simple alternation of successful and unsuccessful year classes since the most important direct competitor of the 0-group is the immediately preceding year class, the I-group. Instead, one observes that successful year classes of Pacific sardine and mackerel arrive in series of years. The sardine has significant runs of 2, 3, 4 and 5 years and the Pacific mackerel has runs of about the same length and with a somewhat greater intensity (Fig. 102). As yet, the causes of these successful sets of year classes have not been identified, but population recruitment can be satisfactorily duplicated by simple auto-correlation simulation (Lenarz, 1971) (Fig. 103).

In the time-series data on scale deposition in the Santa Barbara and Soledad basins (Soutar and Isaacs, 1974) there is no evidence of significant runs of 5-year averages over a 200-year time period (Fig. 104). In addition, there are no correlations between the successes and failures of the total estimated epipelagic fishes and the Pacific hake which dwells below the mixed layer (Fig. 105). The total biomass of these fishes is subject to far less variation than the biomass of the individual species (Table 10).

SPACE SCALES

Rather than the usual spatial scales, I choose to recognize four scales related to the species: the behavioural, the hydrographic, the physiological and the external. By *behavioural*, I mean the scale of aggregation induced by the individual behaviour of the organism. In the clupeids this is the fish school. By *hydrographic*, I mean the scale which attracts and holds fish in a small geographic area like an upwelled water mass, or a rich zooplankton bloom area. By *physiolological*, I mean the distribution of a species, constrained by physiological limits such as temperature tolerance. By *external*, I mean the scale of event by which food or predators enter the environment of a species from outside its distribution area.

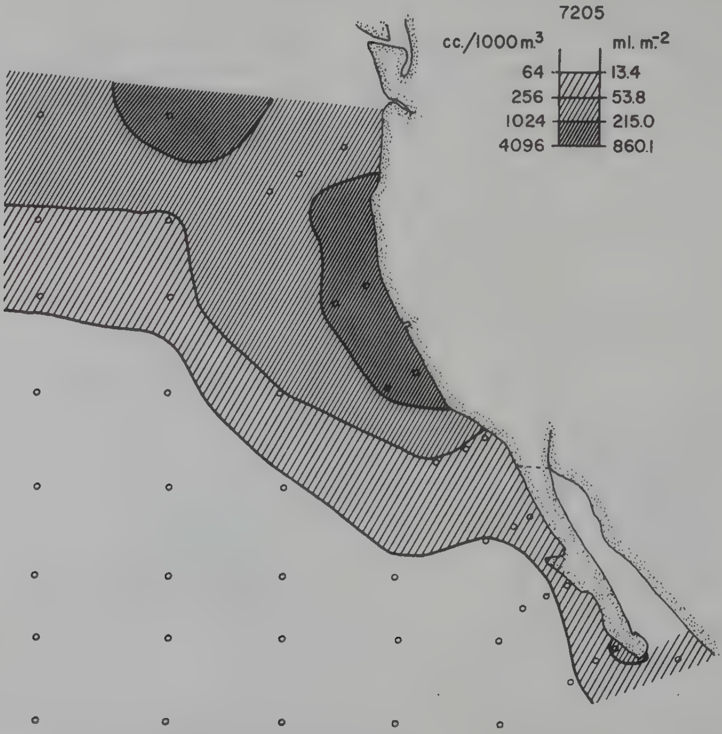

Figure 100. Zooplankton volume off the west coast of North America in April, May and June of 1972. Regions occupied indicated by clear circle. Stations per region were from 3 to 20.

BEHAVIOUR SPACE SCALE

The schooling habit of the major populations of schooling fishes presents a paradox in competition for food among individual, intraspecific competition and limitation of population size. During the decline of the sardine, the schooling habit at spawning time apparently remained, even as the population declined to less than 10 000 tons from a population of 4 million tons.

A schooling fish ultimately depends on the primary productivity in the immediate area of the school whether it feeds on the phytoplankton directly, the herbivores, or the carnivorous and omnivorous species and growth stages of species. The northern anchovy (*Engraulis mordax*) is an omnivore. Anchovy schools frequently contain 15 000 g of fish under each metre of sea surface. The food requirement for a school of this compaction is of the order of 16 g of carbon per square metre of fish school per day. Since this is about 16 times the average primary production under each square metre of sea surface off southern California, the school must move several times its own area each day. While this would require only a trivial amount of swimming by an individual, a large school may be forced to maintain a high steady rate of swimming. I find that fish schools are most common in the 20 to 30 m diameter range, but half of the fish are in schools of 90 m diameter up to an observed maximum of 400 m.

The northern anchovy, an omnivore, achieves its growth and ultimate stock size by succeeding in harvesting a portion of the primary production of its local area by eating phytoplankton, herbivores and other omnivores. Anchovy school size determines the rate at which each anchovy must swim to secure energy for respiration, growth, and reproduction

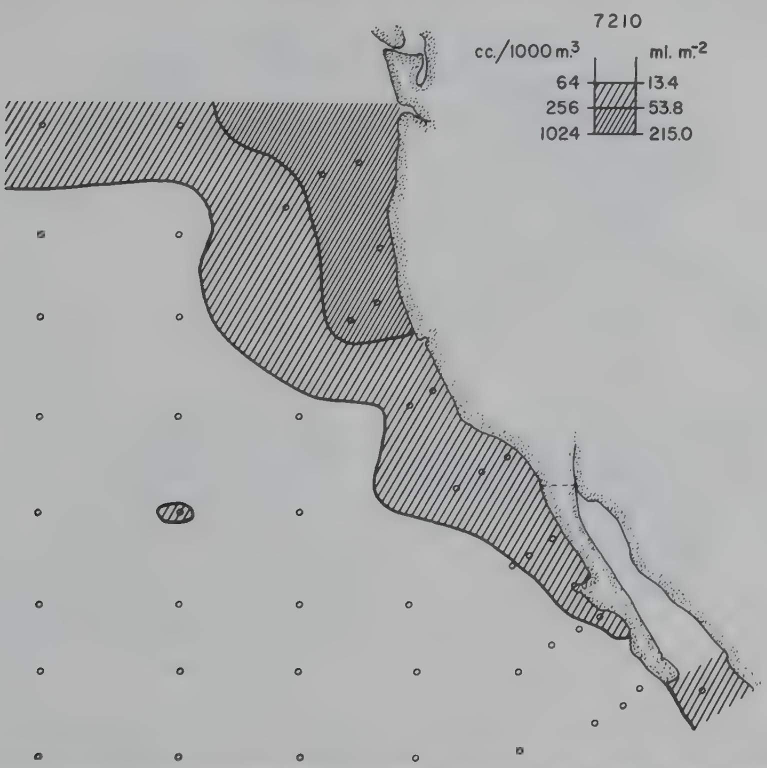

Figure 101. Zooplankton volume off the west coast of North America in September and October of 1972. Regions and stations indicated, the same as in Figure 100.

within the combined constraints of local primary and secondary production and the production of other consumers of that production. For a numerical example, a 200 m diameter school of anchovies with a food chain conversion efficiency of 0·12, in an area with a local primary production rate of 1 g C m^{-2}day^{-1}, and having a compaction of 15000 g per square metre would have to move 21 km per day (or two body lengths per second for the 12 cm anchovy) to maintain parity with the local primary production. This consideration of a single school does not include passing into areas where other schools have just fed, nor repeated entry of the area grazed. While the two body lengths per second seems plausible for individual swimming, feeding activities would slow the mean rate of progress of the school.

I interpret this to mean that the severe food competition imposed by membership in a large fish school

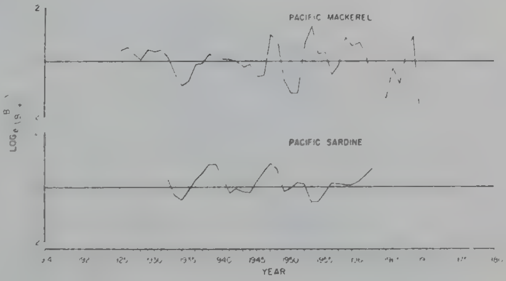

Figure 102. Time series of reproductive success as inferred from annual estimates of age specific biomass (Murphy, 1966; MacCall, in prep.; and MacCall, pers. comm.). The time series indicates significant coherence as estimated from the non-parametric runs test within each species, but no correlation in the reproductive success between species.

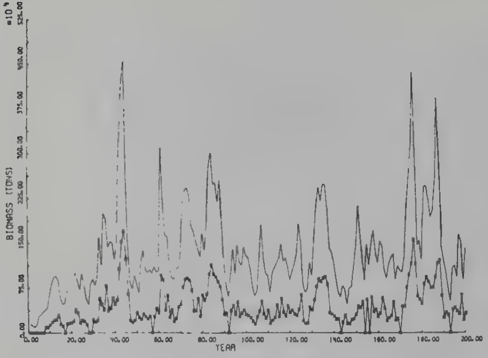

Figure 103. A simulation of the Pacific sardine population for 200 years using the observed random variation and autocorrelation parameters of the Pacific sardine recruitment (Lenarz, 1971) derived from the age specific biomass estimates published by Murphy (1966). Fishing mortality was varied from 0·4 to 0·8 depending on stock sizes in excess of 300 000 tons. Fishing on the simulated stock was stopped if the biomass was below 300 000 tons. Beginning biomass was estimated to be that at 1966 (Smith, 1972) and no fishery was conducted for 8 years.

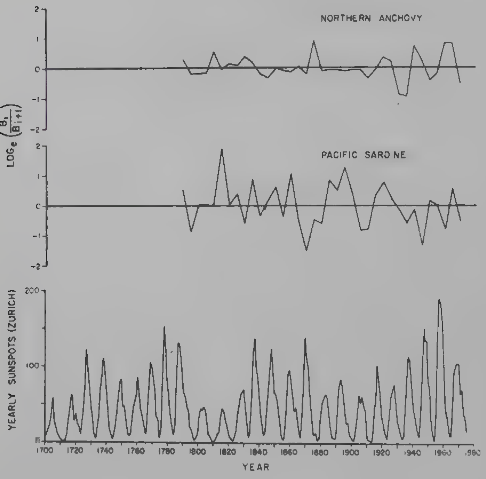

Figure 104. Reproductive success of the northern anchovy and Pacific sardine since 1790 as calculated comparison of biomass (Soutar and Isaacs, 1974) in one 5-year period with biomass in the next 5-year period (Table 9). There is no significant coherence in the series for either species nor is there evidence for correlation either positive (limited productivity) or negative (species competition). Neither do the 11- or 90-year cycles in the sunspot number appear to show agreement with reproductive success on cursory examination.

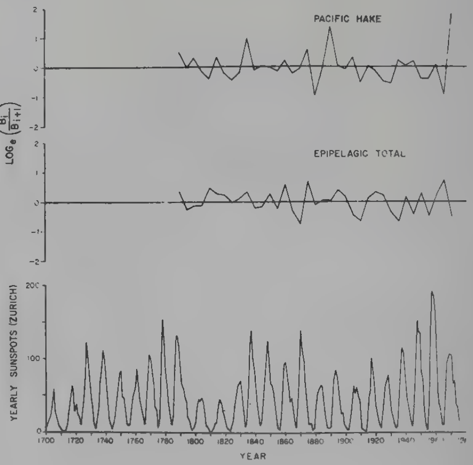

Figure 105. Reproductive success of the Pacific hake below the thermocline with the total 5-year average reproductive success of the epipelagic fishes. Reproductive success estimated from adjacent biomass estimates (Table 9) (Soutar and Isaacs, 1974) as in Figure 104. There is no agreement of the reproductive success of the total epipelagic fish and the Pacific hake, nor are the time series of reproductive success significantly coherent. Agreement of the sunspot cycle maxima in the last four 10-year cycles and the epipelagic total reproductive success minima of the same period does not obtain in the earlier data.

is outweighed by the diminution of predation and the facilitation of reproduction conferred by the schooling habit. The relatively short distances between fish within schools and the long distances between schools raise the possibility that population size limits are imposed by the competition for food between schools rather than the competition for food within schools.

THE HYDROGRAPHIC SPACE SCALE

The school paradox is further heightened by the apparent aggregation of schools into school groups. These school groups (Smith, 1975) are not well defined yet because of our lack of tools to observe underwater phenomena at the 10 km scale. The glimpse afforded by sonar indicates groups of 3500 schools or so in a 10 km diameter area. Such an aggregation of anchovy might contain 1 % of the estimated biomass of the total anchovy stock. The prime characteristic of the school group is that it contains a mixture of fish sizes and ages far broader than that of a school. The hydrographic features which control this scale have not been identified, though features like those

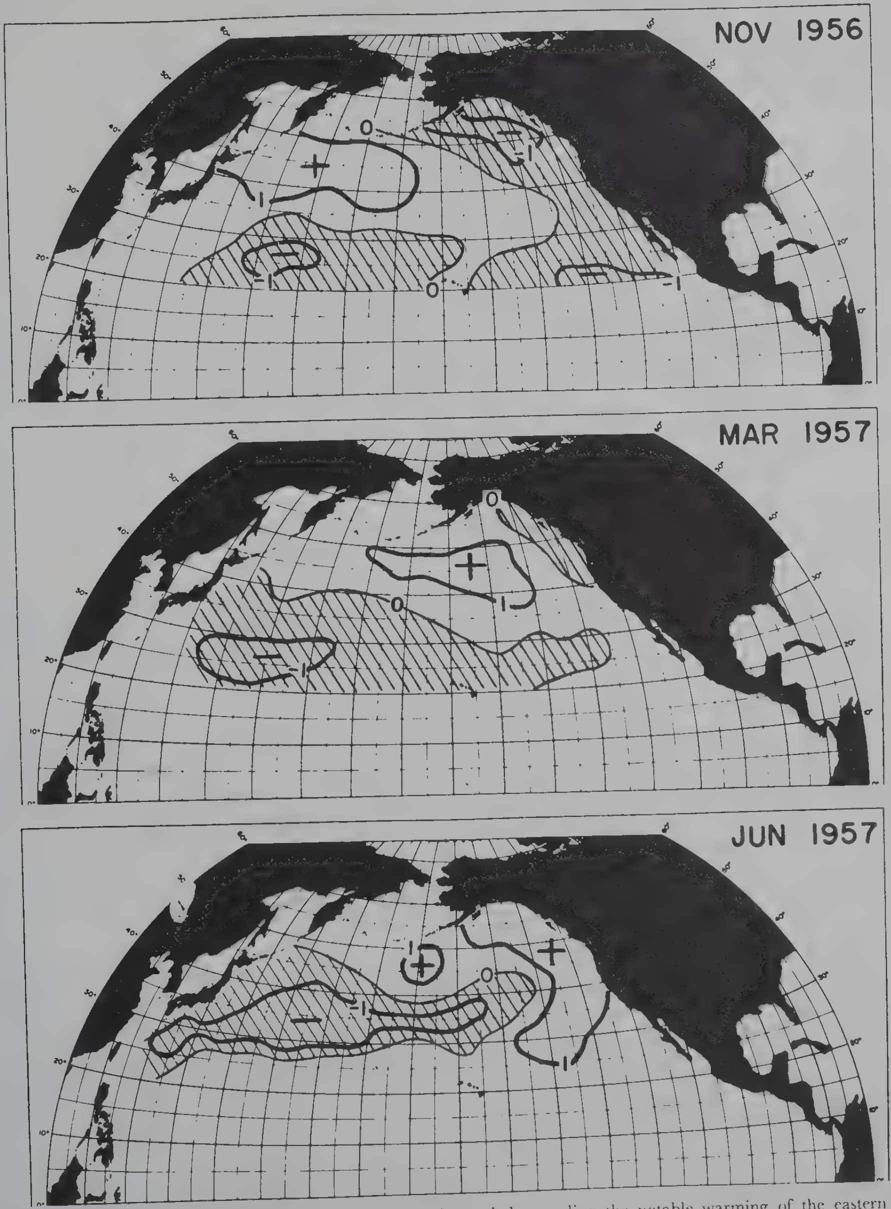
NOV 1956
MAR 1957
JUN 1957
+
−
0
-1
10°
20°
30°
40°
50°

Figure 106. Surface temperature anomalies (Eber, 1971) in the period preceding the notable warming of the eastern temperate Pacific (Sette and Isaacs, 1960).

Table 9. Standing crops of major fish stocks of the California Current as inferred from present day stock sizes and scale deposition rates in the 19th and 20th centuries (thousands of metric tons). Slope and intercept used to convert scale deposition rate to biomass

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Pacific saury	Epipelagic total	Pacific hake	Total
1785	475	3 917	24	105	4 521	4 534	9 055
90	791	5 218	24	328	6 361	7 545	13 906
95	326	4 315	96		4 737	7 447	12 184
1800	326	3 598	96		4 020	10 299	14 319
05	326	3 034	96		3 456	8 824	12 280
10	326	5 068	24		5 418	5 971	11 389
15	2 054	4 909	↓		6 963	8 275	15 238
20	2 151	5 666	↓	751	8 568	6 760	15 328
25	3 082	5 197	↓	110	8 389	4 283	12 672
30	1 704	7 574	↓	55	9 333	3 496	12 829
35	3 975	8 993	60		13 028	8 952	21 980
40	2 823	7 471	60		10 354	8 193	18 547
45	3 264	5 406	24		8 694	8 345	17 039
50	5 798	5 234	24		11 056	8 226	19 282
55	3 944	4 741	42		8 727	7 079	15 806
60	11 093	4 119	24	40	15 276	8 718	23 994
65	6 502	4 213	↓		10 715	7 016	17 731
70	1 464	3 426	↓		4 890	6 549	11 439
75	909	8 428	60		9 397	11 432	20 829
80	500	7 714	24	51	8 289	4 274	12 563
85	1 148	7 205	33	132	8 518	4 168	12 686
90	1 850	6 668	24	40	8 582	15 686	24 268
95	6 504	5 873	51	40	12 468	16 015	28 483
1900	9 177	5 475	33		14 685	14 800	29 485
05	3 882	5 044	33	40	8 999	19 818	28 817
10	1 738	2 770	42		4 550	11 725	16 275
15	2 444	2 598	60		5 102	12 075	17 177
20	5 055	3 690	24	51	8 820	10 264	19 084
25	6 226	4 378	60	51	10 715	6 314	17 029
30	5 300	1 803	150	120	7 373	3 562	10 935
35	2 900	705	132	0	3 737	4 376	8 113
40	2 532	1 477	105	152	4 266	4 482	8 748
45	679	1 862	114	773	2 732	5 375	8 107
50	765	1 208	51	1 535	3 559	3 675	7 234
55	732	986	69	353	2 140	2 447	4 587
60	326	2 168	33	140	2 667	2 535	5 202
65	553	4 755	24	40	5 372	977	6 349
70	326	2 797	24	133	3 280	5 927	9 207
Slope *b*	1 417·37	459·45	90	250		499·39	
Intercept *a*	325·93	96·59	24	0		0	

described in Walsh (1976) do occur at this scale. Small, (pers. comm.) describes diel winds which can generate "newly" upwelled blebs of water. These may foster the aggregation of vertically migratory herbivorous zooplankton which could slow the mean progress of schools. This would cause local aggregations of schools with fish of diverse sizes as observed in school groups thus far.

PHYSIOLOGICAL SPACE SCALE

An important feature of the physiological scale is that physiological limits vary during the life cycle. An example is the Pacific sardine, all of whose viable eggs were spawned in temperatures above 13°C: the adults commonly migrated to areas far colder to the north of the spawning area to feed in the highly productive subarctic and transition waters 1200 miles away. The Pacific hake undergoes a similar migration through the same area, but at ~100 m depth.

EXTERNAL SPACE SCALE

It is still undetermined what the nature and magnitude of influences external to the fishes' own physiological scale might be, but one does not have to look far for interesting examples. The albacore is spawned in the western equatorial Pacific and some proportion

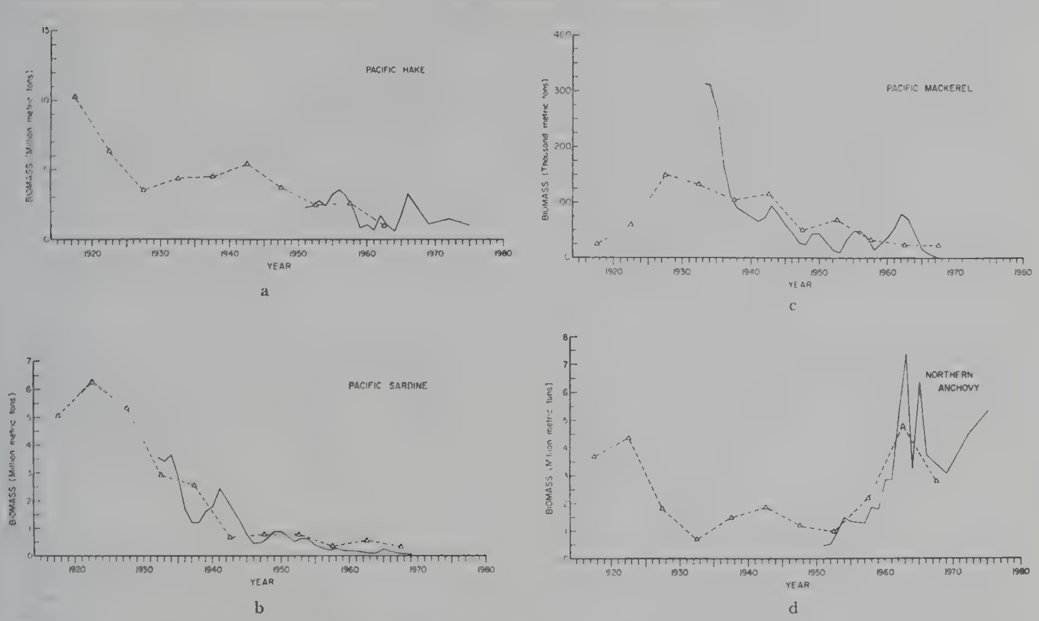

Figure 107a, b, c, d. Time series of biomass of some major species (a, Pacific hake; b, Pacific sardine; c, Pacific mackerel; d, northern anchovy) off the west coast of North America. Dashed lines and triangles at 5-year intervals are from Soutar and Isaacs (1974). Solid line is from annual biomass estimates by fishery analysis or annual (1951–1966) and triannual (1966–1975) estimates from spawning surveys.

of the young migrate through the transition waters to the subarctic, transition and upwelled waters off the North American coast. The predation of these fish on anchovies may approach 15% of the production of the northern anchovy population (Brownell et al, 1976). The north-south shift of albacore (Laurs et al, 1976) catch and the offshore-onshore distribution of anchovy appear to interact broadly. This interaction has sufficient magnitude that the albacore may be an external spatial source of the multi-year cohort changes in reproductive success noted above. Other predators come from outside the anchovy distribution as well. For instance, the northern fur seal predatory capacity has been estimated as 7% of the anchovy production capacity (Brownell et al, 1976).

To estimate the impact of the transpacific migration of albacore from the western tropical Pacific and the migration of fur seals from the Bering Sea, studies of the blocking or guiding effects of the transition zone would be necessary. How dynamic the zone might be at this scale is illustrated by a major warm anomaly of surface temperature (Eber et al, 1968) which moved across the Pacific about 6000 miles and replaced the cold anomaly off the California coast in November 1956 (Fig. 106) and endured there for three years. Eber's (1971) interpretation of this anomaly motion is that a standing wave in the transition zone which alternately causes slight northward and southward displacements of the horizontal thermal gradient of the subarctic to central water mass transition, underwent a gradual phase change. This resulted in the partitioning of the west wind drift water at the coastline so that the water was predominantly transported to the Alaskan gyre rather than the California Current. It is necessary to acquire the ability to translate these major oceanic events to the scale of interest of fish population managers.

ULTIMATE COMMUNITY CARRYING CAPACITY

The fish communities which inhabit the eastern boundary current upwelling zones of the Pacific and of the south Atlantic have strikingly similar species composition. Recent estimates of fish production (MacCall et al, 1976) in the California region indicate that the potential here is somewhat less than the eastern south Atlantic and much less than the Peru–Chile coastline. It also appears (Table 9) that the

Table 10. Crude spawning success ratios in 5-year intervals for pelagic fish off the temperate section of the Pacific coast of North America as estimated from sediment records of fish scales

ln (*R*/*S*)	Proportionate change	Pacific sardine	Northern anchovy	Pacific mackerel	Pacific saury	Epipelagic total	Pacific hake	Total biomass
– 2·0	*X* 0·14	–	–	–	1	–	–	–
– 1·5	*X* 0·22	2	–	1	2	–	–	–
– 1·0	*X* 0·37	4	2	4	2	1	2	–
– 0·5	*X* 0·61	8	4	5	1	9	7	7
0	*X* 1·00	10	23	17	2	17	20	23
0·5	*X* 1·65	8	5	4	1	10	5	7
1·0	*X* 2·71	3	3	5	4	–	1	–
1·5	*X* 4·48	1	–	1	1	–	1	–
2·0	*X* 7·39	1	–	–	–	–	1	–
Number.		37	37	37	14	37	37	37
Mean.		– 0·01	0·04	0·01	– 0·11	– 0·01	0·04	0·00
Standard deviation . . .		0·778	0·447	0·661	1·147	0·399	0·582	0·312

California Current area is in a relatively low biomass era for the fish stocks of interest. It is interesting to examine together the biomass time series from scale deposition rates (Soutar and Isaacs, 1974), spawning surveys (Smith, 1972) and fishery analysis (Murphy, 1966; MacCall, in prep.). The scale deposition series is very important because it allows us to use existing brief relationships between biomass estimates to see time series over two centuries. This permits the perspective of natural fluctuations so that possible chronic effects of fishing or environmental change by man can be viewed in the context of natural variation (Longhurst et al, 1972).

Examination of the long-term record does not reveal any substantive effects which can be attributed to the major El Niño years, sunspots, or the volcanic activities in the late 19th century. Of the highest interest in the context of ultimate community carrying capacity, the Pacific hake (Fig. 107a), Pacific sardine (Fig. 107b) and Pacific mackerel (Fig. 107c), are all presently low with respect to their levels early in this century. The sardine and mackerel were subjected to intensive fisheries in the 1930's and the Pacific hake was unfished until the mid-1960's. The northern anchovy now appears to be as high in population as the 1920's scale index (Fig. 107d). Classical ecological theory would indicate that the replacement of stocks of low reproductive capacity by stocks of high reproductive capacity may be one indicator of environmental disturbance.

One can see from the 200-year frequency of proportionate changes in the population in Table 10 that the anchovy is the least variable of the fish stocks at 5-year intervals. If ecological theory concerning high reproductive rate holds, this means that the California Current area is one of almost continual environmental disturbance favouring the anchovy. Occasionally, one can observe an outbreak of stability which favours the longer lived stocks with moderate reproductive rates.

The overall minimum in standing stocks is in the 1955 (1949–1954) 5-year period. It is reasonable to ascribe the depth of this nadir, a factor of 2·5 below the previous total biomass minima in 1870 and 1810, to the combined presence of heavy fisheries and low overall productivity. It seems plausible that the decline beginning in 1930–1935 might have been arrested by the high reproductive success observed in the late 1930's had not a massive fishery intervened (Table 9).

The major objective of the CalCOFI (California Cooperative Oceanic Fisheries Investigations) has been to determine the causes of the large fluctuations in fish populations off the west coast of North America. The decline of the Pacific sardine has been observed with scales in varved sediments and fishery analysis. The increase in the northern anchovy has also been observed with scales from varved sediments and spawning surveys. Other massive populations, the jack mackerel and the Pacific hake, have been discovered. It still remains to resolve these features, described at haphazard scales of space and time, in terms of the requirements for wise management of resources in the face of environmental change.

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Precision of sonar mapping for pelagic fish assessment in the California Current

Paul E. Smith

National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038, U.S.A.

A large scale sonar map of fish schools in the Los Angeles Bight is described and used to determine the amount of sampling required to estimate the number of schools at various levels of precision. About 8 nautical square miles (2744 ha) must be directly surveyed to get an estimate of fish schools with a 25% level of precision: 47 nautical square miles (16121 ha) must be sampled for a 10% level of precision using the observations and assumptions of this paper. Although spatial auto-correlation indicates independent observations can be taken at 5 nautical miles (9 km) spacing or greater, there is a possibility of exclusion or reduction of the number of schools at 7 to 15 nautical miles (13 to 28 km) range which should be further investigated.

Introduction

Sonar mapping (Smith, 1970) has been used to study the distribution, abundance, and size of fish schools in the upper mixed layer of the ocean. Hewitt, Smith and Brown (1976) described detailed methods on field use of sonar to measure the horizontal sizes of fish schools, number of schools per unit surface area, estimated target strength, and estimated school biomass compared to biomass measured by directed purse seine capture of fish schools. The results of several years of acoustic surveys in the California Current area by the California Department of Fish and Game were published by Mais (1974). This paper describes the "patchy" or contagious distribution of fish schools, estimates the degree of auto-correlation of fish school abundance estimates on transect surveys, calculates the sampling effort necessary for the various degrees of sample estimate precision, and approximates the optimum spacing of transects.

Methods

On 20 and 21 December 1971, a transect of 63 nautical miles was conducted in the southern California Bight on the RV "David Starr Jordan" between Malibu and Oceanside through the Santa Catalina Channel. The acoustic equipment was a 580-10 Simrad 11 kHz transceiver attached to a transducer whose acoustic dimensions were a 10° conical beam between the 3 dB down points. An uncalibrated transducer was contained in a fibre glass faired housing which was supported by a conductor cable at a depth of about 10 m while under tow at approximately 3·6 knots. Approximately 8·5 kW power was used at 30 ms pulse lengths. The receiver was set on "reverberation controlled gain" and recordings were collected for distances to 2650 m laterally from the vessel, the NOAA/NMFS RV "David Starr Jordan."

The species of fish in the schools were unknown. However, in the 5 months (October–February, 1971–1972) surrounding this study period, a local fleet of small purse seiners landed 42 500 metric tons of fish from the general area, two-thirds of which was northern anchovy (*Engraulis mordax*) and one-third of which was jack mackerel (*Trachurus symmetricus*) (Oliphant, 1973; Pinkas, 1974).

Results

A total of 1729 targets were recorded and logged from Figure 1. Each target was assigned to a range band of 50 to 500 m, 500 to 1000 m, 1000 to 1500 m, 1500 to 2000 m, 2000 to 2500 m, or 2500 to 2650 m. The range band 0 to 50 m was eliminated from these results because the pulse train of 30 ms was approximately 45 m long and the receiver did not permit

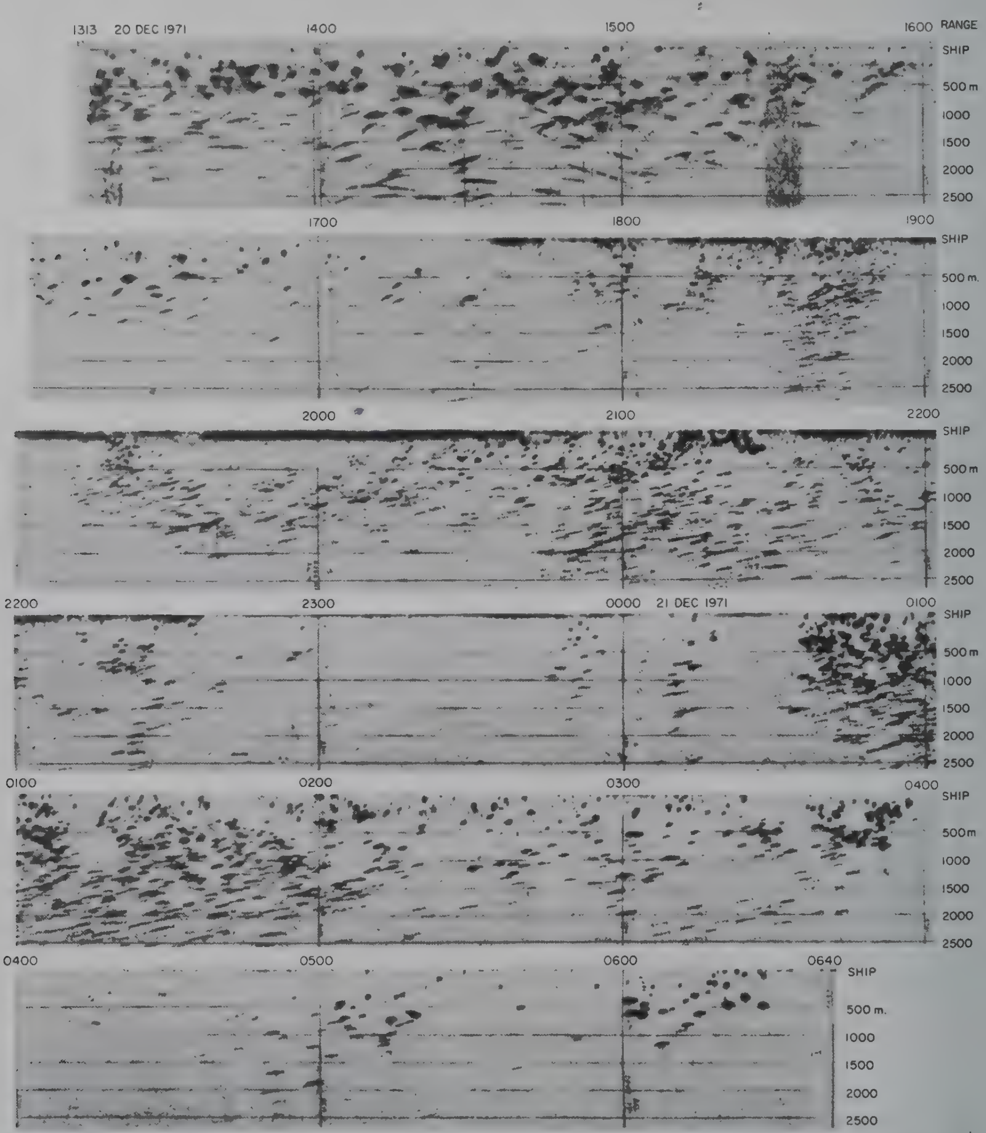

Figure 1. Plan view display of sonar targets in the Santa Catalina Channel off southern California in December 1971. A continuous track extending 63 nautical miles recorded in about 17·5 h. The range scale normal to the ship's course is exaggerated approximately × 2½ relative to the range parallel to the ship's course. Target shapes are, in addition, distorted normal to the ship's course by the 30 ms pulse length. Target shapes are further distorted to a degree relative to range from the ship by the effective beam angle of transmission and reception of 10° between the 3 dB down points.

Table 1. Numbers of sonar targets of fish schools in different range gates observed in the Santa Catalina Channel, December 1971

Track segment nautical miles	Range gates in m 1 50 to 500	2 500 to 1000	3 1000 to 1500	4 1500 to 2000	5 2000 to 2500	6 2500 to 2650
0 – 2·6	30	27	21	7	3	0
2·6– 6·2	31	26	16	11	13	6
6·2– 9·8	23	16	10	8	4	0
9·8–13·5	24	18	7	1	0	0
13·5–17·1	14	15	2	4	3	1
17·3–20·7	57	47	28	11	7	4
20·7–24·3	24	30	29	12	1	0
24·3–27·9	68	42	30	16	12	0
27·9–31·6	58	44	42	32	16	5
31·6–35.2	17	21	11	6	4	2
35·2–38·8	9	5	2	1	0	0
38·8–42·4	60	34	23	22	10	0
42·4–46·0	76	56	50	33	18	9
46·0–49·7	39	19	25	15	2	1
49·7–53·3	52	40	12	10	8	2
53·3–56·9	5	5	4	3	2	0
56·9–60·5	7	14	7	1	0	0
60·5–62·9	22	7	2	0	0	0

the discrimination of schooled targets within the duration of the outgoing pulse. An automatic time marker was used to divide the record into 1 h or 3·6 nautical mile segments of track. Thus the basic unit of count was a rectangle, 500 m × 6700 m, slightly smaller than 1 square nautical mile. Table 1 lists the numbers of targets counted from each unit. In Table 2, boundary range bands, i.e. 50 to 500 m, 2500 to 2650 m, and the first and last transect segments and all other values, have been adjusted to the equivalent values per square nautical mile.

At the same time as this sonar transect, a commercial fish spotter aeroplane flew over the area as part of another programme to measure and identify schools of pelagic fish by aerial surveys (Squire, 1972). In Figure 2, the track of the commercial fish spotter is shown with notes on the identification and location of fish concentrations. Two areas labelled "scattered anchovy" occurred along the track of the RV "David Starr Jordan" and it seems likely that this species comprises most fish in the record shown in Figure 1. Schools recorded by sonar between 2230 and 0200 h, were flown over by the aeroplane but were not observed by the pilot. These schools may have been below the depth at which they could be observed from the air.

Statistical summaries of targets in the range bands listed in Table 2 lead to the postulation that there is a regular decrease in the mean number of targets per unit area with each increment in range. An exponential curve was calculated to give a satisfactory fit to these data as in the following equation:

$$\hat{Y} = b \exp^{mR}$$

where $\hat{Y}$ is the number of schools estimated per unit area corrected for range dependent loss of targets, b is the 0 intercept, m is the slope, and R is the range from the vessel, in metres. The parameters for this series of observations are:

$$b = 53{\cdot}6$$
$$m = -0{\cdot}000912.$$

The correlation coefficient is −0·99, and the exponential model accounts for 98% of the variation. This expression is expected to be appropriate for this time and place. New range loss equations would be needed for other areas and seasons (Smith, 1977).

Table 3 lists the observed values in number of schools per square nautical mile, adjusted to the mean values at zero range. Range gates 5 and 6 were omitted due to the increasing incidence of "zero" observations. It may be useful to manipulate the parameters of the distribution of 72 of the values to gain an estimate of the sampling effort necessary to gain desired levels of precision.

Table 2. Numbers of sonar targets of fish schools observed in different range gates in the Santa Catalina Channel off southern California, December 1971. (Targets per nm^2.)

Track segment nautical miles	Range gates 1	2	3	4	5	6
0 – 2·6	47	38	30	10	4	0
2·6– 6·2	35	27	16	11	13	20
6·2– 9·8	26	16	10	8	4	0
9·8–13·5	27	18	7	1	0	0
13·5–17·1	16	15	2	4	3	3
17·1–20·7	65	48	29	11	7	14
20·7–24·3	27	31	30	12	1	0
24·3–27·9	77	43	31	16	12	0
27·9–31·6	66	45	43	33	16	17
31·6–35·2	19	21	11	6	4	7
35·2–38·8	10	5	2	1	0	0
38·8–42·4	68	35	24	23	10	0
42·4–46·0	86	57	51	34	18	31
46·0–49·7	44	19	26	15	2	3
49·7–53·3	59	41	12	10	8	7
53·3–56·9	6	5	4	3	2	0
56·9–60·5	8	14	7	1	0	0
60·5–62·9	38	11	3	0	0	0
n	18	18	18	18	18	18
$\bar{x}$	40·22	27·17	18·78	11·06	5·78	5·67
s_x	25·04	15·64	14·77	10·20	5·80	9·02
$\overline{\ln \bar{x}}$	3·446	3·096	2·525	1·993	1·692	2·249
$S_{\ln x}$	0·802	0·725	1·040	1·144	0·880	0·869

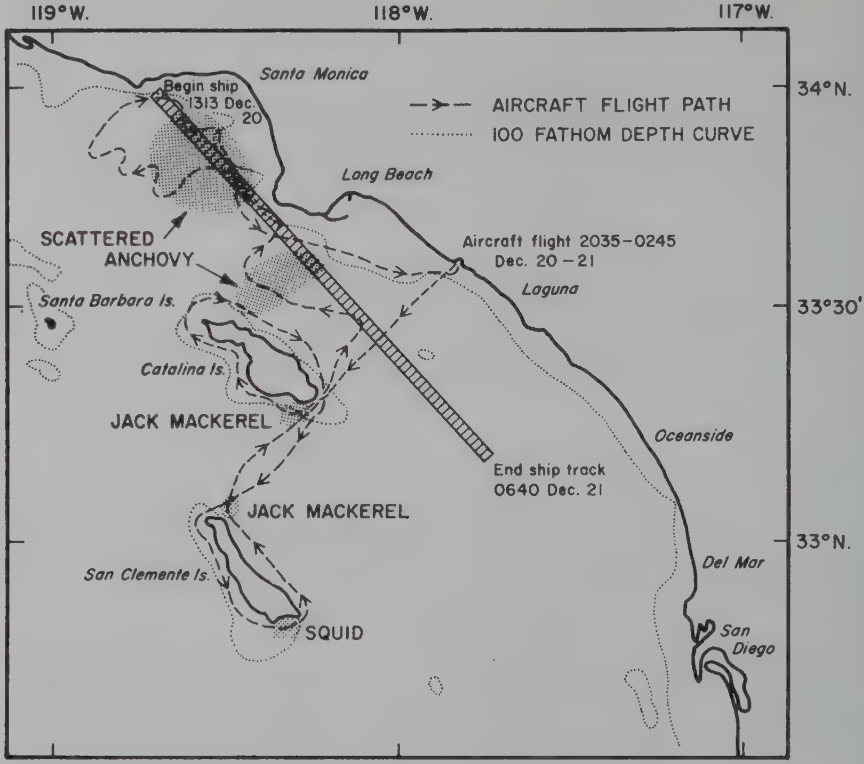
119°W.
118°W.
117°W.
34°N.
33°30'
33°N.
AIRCRAFT FLIGHT PATH
100 FATHOM DEPTH CURVE
Santa Monica
Begin ship 1313 Dec. 20
Long Beach
SCATTERED ANCHOVY
Aircraft flight 2035–0245 Dec. 20 – 21
Laguna
Santa Barbara Is.
Catalina Is.
JACK MACKEREL
Oceanside
End ship track 0640 Dec. 21
JACK MACKEREL
Del Mar
San Clemente Is.
SQUID
San Diego

Figure 2. Diagram from the flight log of an aerial observer during the period of the sonar transect illustrated in Figure 1. The sonar transect is drawn to scale on the chart. The flight path is illustrated with dashed lines. Fish concentrations spotted from the airdraft are shaded. The concentrations crossed by the sonar transect were labelled "scattered anchovy" by the observer in the aeroplane.

One of the statistical distributions commonly referred to in counts of organisms is the log-normal distribution (Bagenal, 1955) in which individual counts are transformed from a variate x to a variate y by the following equation:

$$y = \ln x$$

and the observed parameters, $\bar{y}$ and the standard deviation of y (S_y) have been used to create random log-normal distribution by use of a brief random normal numbers table with 0 mean and unit standard deviation (Dixon and Massey, 1969, Appendix Table 2, p. 451) and the following equation:

$$\hat{X}_i = \exp(V_i S_y + \bar{y})$$

where $\hat{X}_i$ is a derived number of fish schools per square nautical mile for quadrat (i), V_i is the table value of a random normal number list, S_y is the standard deviation of y, and $\bar{y}$ is mean value of all y's.

The observed values and 10 sets of 50 random log-normal values are in Table 4. The mark values are first a threshold value (T) and then successive geometric means of groups which comprise a table for obtaining unbiased estimates of the arithmetic mean of a set of log-normal distributed set of numbers in the original values of number of schools per square nautical mile. A chi-square comparison of target density frequencies (Table 5) shows that the fit of the log-normal model is not adequate. The higher concentrations of fish schools occur more often in the random log-normal sets than in the observed set of

Table 3. Number of sonar targets of fish schools in different range gates in the Santa Catalina Channel off southern California, December 1971. (Targets per nm^2.)

Track segment nautical miles	Range gates 1	2	3	4	1000 m average
0 – 2·6	60	74	93	49	69
2·6– 6·2	44	53	50	54	50
6·2– 9·8	33	31	31	39	34
9·8–13·5	34	35	22	5	24
13·5–17·1	20	29	6	20	19
17·1–20·7	83	94	90	54	80
20·7–24·3	34	61	93	59	62
24·3–27·9	98	84	96	78	89
27·9–31·6	84	88	133	161	117
31·6–35·2	24	41	34	29	32
35·2–38·8	13	10	6	5	9
38·8–42·4	86	69	74	112	85
42·4–46·0	109	112	158	166	136
46·0–49·7	56	37	81	73	62
49·7–53·3	75	80	37	49	60
53·3–56·9	8	10	12	15	11
56·9–60·5	10	27	22	5	16
60·5–62·9	48	22	9	0	20
$\bar{x}$	51·06	53·17	58·17	54·06	54·17
s_x	31·82	30·64	45·80	49·71	37·13
$\overline{\ln x}$	3·6857	3·7691	3·6507	3·5860	3·7201
$S_{\ln x}$	0·7970	0·7198	1·0506	1·1343	0·8160

fish school concentrations from which the log-normal parameters were generated. From Table 6 one also may note that the standard deviation of the log-normal random number sets is higher than the observed in 9 out of 10 trials. Until these tendencies are understood, the log-normal approximation to the sample distribution of the number of schools per

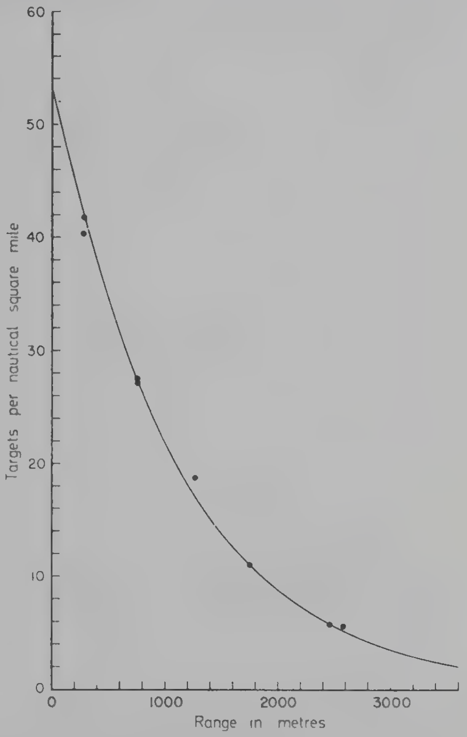

Figure 3. Apparent range-dependent target loss, as estimated from targets per square nautical mile (Table 3). $y = 53{\cdot}6 \exp(-0{\cdot}000912\ R)$ where R is the range in metres. Correlation coefficient −0·99. Points are Table 2 values and the line is a least squares fit.

Table 4. Comparison of school densities (numbers per nm^2) from observations and from 10 sets of random numbers generated with observed log-normal parameters (grouped).

Mark	Obs.	1	2	3	4	5	6	7	8	9	10
T	1	–	–	1	–	–	–	–	–	–	–
2·7	–	–	1	1	–	–	–	–	–	1	–
4·5	3	–	1	0	1	–	–	–	–	1	–
7·4	4	1	2	4	1	–	3	3	3	1	2
12·2	6	4	7	1	7	7	3	4	2	6	7
20·1	6	4	8	12	5	10	8	7	8	5	8
33·1	14	13	10	13	12	8	17	14	9	12	8
54·6	13	11	10	10	14	13	10	9	9	9	7
90·0	21	9	6	6	6	6	4	6	12	10	13
148·4	4	6	4	2	2	4	4	4	5	3	4
244·7	–	1	0	–	1	1	0	2	1	1	1
403·4	–	0	0	–	1	1	1	1	0	1	–
665·1	–	1	1	–	–	–	–	–	1	–	–
Mean	54	76	56	43	60	61	52	63	76	63	58
Group mean	55	76	59	43	57	61	54	64	75	61	58

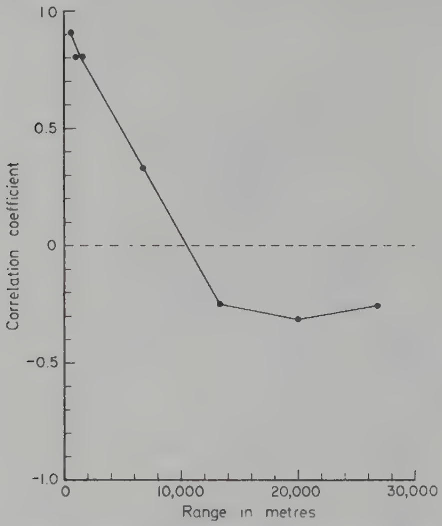

Figure 4. Spatial auto-correlation coefficients for adjacent square nautical mile quadrats and quadrat centres spaced 1000, 1500, 6667, 13334, 20002, and 26669 m apart. Data pairs are derived from Table 3.

nautical square mile must be used with caution. As larger sets of data become available study should be given to more effective probability generating functions of the number of schools per unit area.

Table 5. Chi-square analysis of the observed distribution of sonar targets and a simulated log-normal distribution using the same parameters.

Schools per nm²	Observed	Expected	(Difference)² Expected
9·5	8	3·88	4·37
12·2	6	6·91	0·12
20·1	6	10·80	2·13
33·1	14	16·70	0·44
54·6	13	14·69	0·19
90·0	21	11·23	8·50
148·4	4	7·77	1·83
Chi-square			17·59
Probability (6. d.f.)			0·99 > *P* > 0·995

Patches

An important feature of the distribution of fish schools is that they are "patchy." The mathematical description of this "patchiness" of schools is quite dependent on the scale of the natural pattern being observed and the arbitrary scale of the sample quadrats (Pielou, 1969, p. 147). Thus the results presented here are specific for rectangular quadrats of 1 square nautical mile.

The count of targets in a quadrat was correlated with the number of targets in an adjacent quadrat. Highly positive spatial auto-correlation coefficients were common for the series of adjacent quadrats whose centres are separated by 500 m (Table 7). The coefficient also decreases toward zero with increasing distance as expected. The spatial auto-correlation plot (Figure 4) suggests that the abundance of fish school in quadrats separated by a distance of 10 000 m is independent. All auto-correlation points (12) at greater distances than 10 000 m are negative. This is either a statistical artifact or means the presence of a group of schools may diminish the probability that another group of schools will occur within 13 to 27 km.

Table 6. Parameter estimates from ten sets of fifty random log-normal numbers based on observed parameters

					Grouped			
	Mean	S.D.	Mean log	S.D. log	Mean	S.D.	Mean log	S.D. log
Observed	54·11	39·60	3·6741	0·9201	54·85	38·25	3·6761	0·9223
Random 1	75·62	87·98	3·9492	0·8444	76·56	98·06	3·9200	0·8652
Random 2	56·12	82·98	3·4937	1·0240	58·88	64·01	3·5200	0·9844
Random 3	43·27	33·39	3·4504	0·8900	42·83	32·93	3·4694	0·8191
Random 4	60·29	73·48	3·6104	0·8811	56·89	65·70	3·6500	0·8763
Random 5	61·48	70·19	3·7196	0·8722	60·85	68·03	3·7200	0·8521
Random 6	51·93	55·57	3·6027	0·8067	53·71	62·49	3·6200	0·8179
Random 7	62·97	66·32	3·7023	0·9536	63·86	72·99	3·7200	0·9212
Random 8	76·04	115·97	3·8582	0·9260	74·57	98·14	3·8700	0·9303
Random 9	62·55	72·55	3·6738	0·9948	61·41	67·64	3·6800	0·9833
Random 10	57·69	46·61	3·6931	0·9148	58·33	48·91	3·7100	0·8927

Table 7. Spatial auto-correlation coefficients between counts of pelagic shoals within quadrants separated by ranges of 500 to 30 000 m.

Distance between quadrat in m	Coefficients	Median
500	0·901; 0·872; 0·901	0.901
1 000	0·806; 0·795; 0·860	0·806
1 500	0·802	0·802
6 667	0·129; 0·084; 0·383; 0·348; 0·335	0·335
13 334	−0·230; −0·081; −0·256; −0·250	−0·240
20 002	−0·309; −0·314; −0·403; −0·312	−0·312
26 669	−0·261; −0·246; −0·272; −0·037	−0·254

Discussion

This study shows that a group of horizontal records of fish schools obtained acoustically or from aerial surveys (Squire, 1972), can be of considerable use in the design, conduct, and subsequent analysis of echo sounder and sonar surveys. The primary result of the record described here is that the standard deviation of the number of schools in a 1 square nautical mile quadrat count is about 70% of the mean. To obtain a more precise estimate of the mean number of schools per unit area one must obtain several relatively independent samples of the number of fish schools per unit area. One way to calculate the number of samples needed for this "patchy" distribution is by use of the mean of this set of samples and *k* of the negative binomial equation with the following equation (Southwood, 1966, p. 20):

$$N = (\bar{x}^{-1} + k^{-1})/D^2$$

where $\bar{x}$ = the arithmetic mean of the samples
k = the exponent of the negative binomial
D = the required level of accuracy expressed as a decimal (10% = 0·1 for example)
N = number of samples required.

A first estimate of *k* may be obtained from the sample mean and sample variance (Table 3):

$$\begin{aligned} k &= \bar{x}^2/(S^2 - \bar{x}) \\ &= 54{\cdot}17^2/(1378{\cdot}64 - 54{\cdot}17) \\ &= 2{\cdot}22 \end{aligned}$$

Therefore the required number of square nautical mile samples (N) for various levels of precision (D) are:

D	N
1%	4690
5%	188
10%	47
25%	8
50%	2

Variance in target count has been assumed to be solely from patches. This example may include variations from other calculable sources, such as internal waves. Thus, these may be overestimates of the sample number required after correction for range dependent losses.

If negative binomial parameter estimates are not feasible or necessary, the same sample requirements may be specified by

$$N = \frac{S^2}{D^2\,\bar{x}^2}.$$

Auto-correlation analysis indicates that for this record, samples 5 nautical miles apart approach independence. To survey a square nautical mile as it is presently done with a 250 m wide transect (0·135 nautical mile) would require a transect length of 7·4 nautical miles, thus a sample unit would be approximately 12·4 nautical miles. Sampling should be conducted at 12·4 knots for about 35 minutes of each hour according to this approach. If data were grouped into 8 h units, the precision of the mean concentration should be about 25%. Fifty schools per square nautical mile is in the upper range of concentrations (Mais, 1974) in the California Current and lower concentrations of schools should yield better precision with this kind of distributional assumption (negative binomial).

This analysis can also be used as a method for determining the optimum tactics to be used to find commercial concentrations of fish. The spatial auto-correlation indices indicate that search for school concentrations at intervals closer than about 5 nautical miles tend to be redundant regardless of the method of search.

These observations on school groups also raise important questions regarding the biological function of the "patchy" distribution of school groups and the spaces between school groups. In particular, the observation that the presence of a group of schools may diminish the probability that another group of schools will occur within 13 to 27 km (7 to 15 nautical miles) requires further observations. If this result is supported by more extensive observations, it could lead to increased understanding of the impact of these groups of schools on the waters they occupy and the way in which the carrying capacity of the environment limits population size of pelagic schooling fish. Direct studies on the impact of a group of schools on the water they occupy and on the avoidance of previously occupied areas would be of considerable value.

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POSITION OF LARVAL FISH IN AN ECOSYSTEM

PAUL E. SMITH and REUBEN LASKER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service, Southwest Fisheries Center
P.O. Box 271, La Jolla, California 92038, U.S.A.

First order estimates of distribution, abundance, growth and survival rate of the northern anchovy larva are used to examine the interactions of the larval stage and its environment and how these regulate the northern anchovy population.

Changes in the degree of spawning of anchovy are compared to the seasonal and annual variations in seawater temperature, vertical temperature gradients, upwelling, California Current speed, flushing rate of the southern California Bight, and secondary production. It appears that the usual habit of the anchovy to spawn heavily in the southern California area in winter, alters radically in some years. The cause for this is not yet known.

Quarterly apparent mortality rates are assembled for the years of greatest environmental changes in the southern California regions for anchovy eggs and larvae (to 6·5 mm in length). Information needed for analysing the causes of anchovy larval mortality has been assembled. For example, first-feeding anchovy larvae require abundant food in a narrow size range (30 to 50 μm). Tests with laboratory-reared larvae have confirmed the need for larval food organisms at proper concentrations (> 30/ml) to insure adequate feeding. In nearshore waters, these are associated with chlorophyll maximum layers at 15 to 30 m depth off California. Upwelling was observed to disperse the food organisms until they were too low in number to support larval anchovy growth.

INTRODUCTION

In the past three decades, 1946 to 1976, the northern anchovy has replaced the Pacific sardine in biomass (Smith, 1972) and in the commercial reduction and baitfish fisheries off the California coast (Baxter, 1967; Messersmith, 1969; Ahlstrom, 1966). The northern anchovy is now the chief forage fish for the sport fishes, large commercial fishes, marine mammals, and marine birds of the California and the northeast Pacific. The disappearance of the Pacific sardine and the appearance of the massive anchovy population has sustained a large research effort to determine the causes of the major fluctuations of the fish populations off the Pacific coast of North America. This report combines results from theoretical, field and laboratory studies of the northern anchovy, particularly the causes of reproductive success. The primary impetus for these studies stems from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) in field and laboratory work begun in 1947.

It now appears that the fishery on the central subpopulation of the northern anchovy (Fig. 65) will increase before we gain a functional understanding of the causes of rapid decline in pelagic stocks. Because of the socio-economic issues involved, a fishery on the anchovy will likely be carefully regulated. We intend to use this period of cautious harvest to study features of the biological and physical environment of the anchovy which are associated with reproductive success. Specifically, we will use a selection of cause and effect relationships in the description of reproductive success. Minimal criteria for that success will be established through theoretical models, designed from and verified by field studies and laboratory experiments.

GENERAL PRODUCTIVITY OF THE ANCHOVY LARVA ENVIRONMENT

Although the ability to measure the primary productivity of a representative area of the California Current exists (see, for example, Owen, 1974), there is no long-term record. However, estimates of secondary production are possible by the observation of zooplankton displacement volume. The absence of adequate descriptions of zooplankton populations which make up this diverse assemblage, does not permit a quantitatively satisfactory model for this area. Therefore, fluctuations are presented as mean seasonal cycles of zooplankton displacement volumes with year-to-year differences.

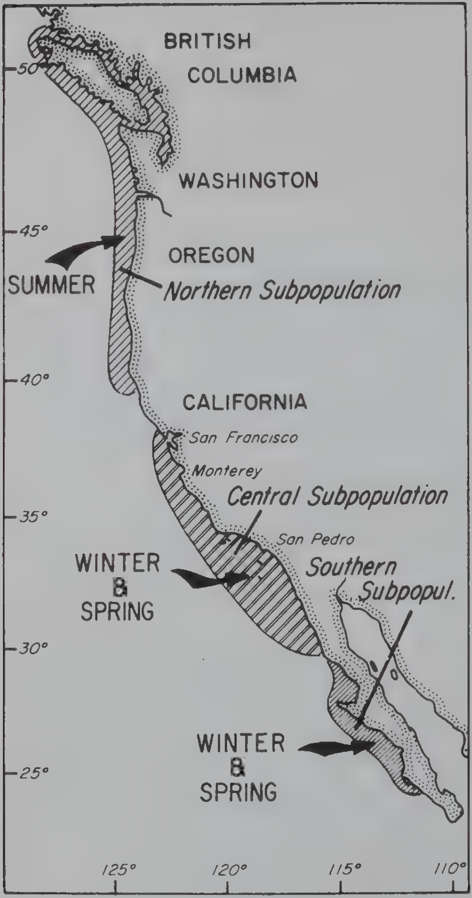

Figure 65. The major spawning seasons and areas of the three sub-populations of the northern anchovy *Engraulis mordax* off the temperate west coast of North America, modified from Vrooman and Smith (1971).

Representative primary production rates (Owen and Sanchez, 1974) for 1969 indicate that the entire habitat of the northern anchovy is probably much less productive than the Peru Current system. In the 80000 n m^2 (275000 km^2) usually occupied by the central sub-population, the annual productivity in 1969 was 490 mg C/m^2/day. Values as high as 1300 mg C/m^2/day were seen occasionally. The maximum seasonal productivity for the entire region was 800 mg C/m^2/day in February–March and the minimum was 260 mg C/m^2/day in November–December. Productivity in the area of the Peruvian anchoveta is usually stated in the range of 1000 to 10000 mg C/m^2/day (Walsh, 1976) and during the "El Niño" phenomenon of 1972, it fell to 300 mg C/m^2/day (Guillen, 1974).

SEASONAL CYCLES

Solar radiation. In Figure 66, it may be seen that the actual average peak in solar radiation is in April because the clear sky solar radiation is strongly modified by cloud cover (Clark et al, 1974). Minimum solar radiation does coincide with the winter solstice. Peak cloud cover coincides with peak upwelling as estimated from the Bakun (1973) barometric pressure model.

Temperature. Temperatures representative of the upper layers of the ocean inhabited by the anchovy commonly vary 4 to 6°C under the influence of water transport from the subarctic water mass, the central water mass, subtropical water mass, upwelling, and seasonal changes in local warming and cooling rate. The 10-m depth peak temperature is commonly attained in August, but a 30-m peak is reached in October–November due to the apparent influence of upwelling. Average minimum temperatures at 30 m occur in July, following the maximum in local upwelling rate. The 10 to 30 m temperature difference indicates two important phenomena for larvae: in January, the temperature difference is minimal, offering the best chances for mixing, and in July, the temperature difference is at a maximum indicating that upwelling and warming are at a joint maximum. Both the minimum and maximum 10 to 30 m temperature difference appear to be detrimental to the formation of feeding layers for larvae and maintenance of patches.

UPWELLING AND CALIFORNIA CURRENT INDICES

Upwelling and the transport offshore of surface waters which it entails (Bakun, 1973) is at a maximum in June and at a minimum in December. One may expect upwelling to add nutrients to the upper layers, to transport nearshore organisms offshore, and to destroy stratification locally. In general, the effect of upwelling should be to favour the adults of a species, but to be inimical to the embryos and larvae.

The California Current rate of flow appears to have a distinct minimum in January and a rather prolonged, but moderate, maximum from March to November. In general, the combined effects of upwelling, offshore transport, and southerly drift would

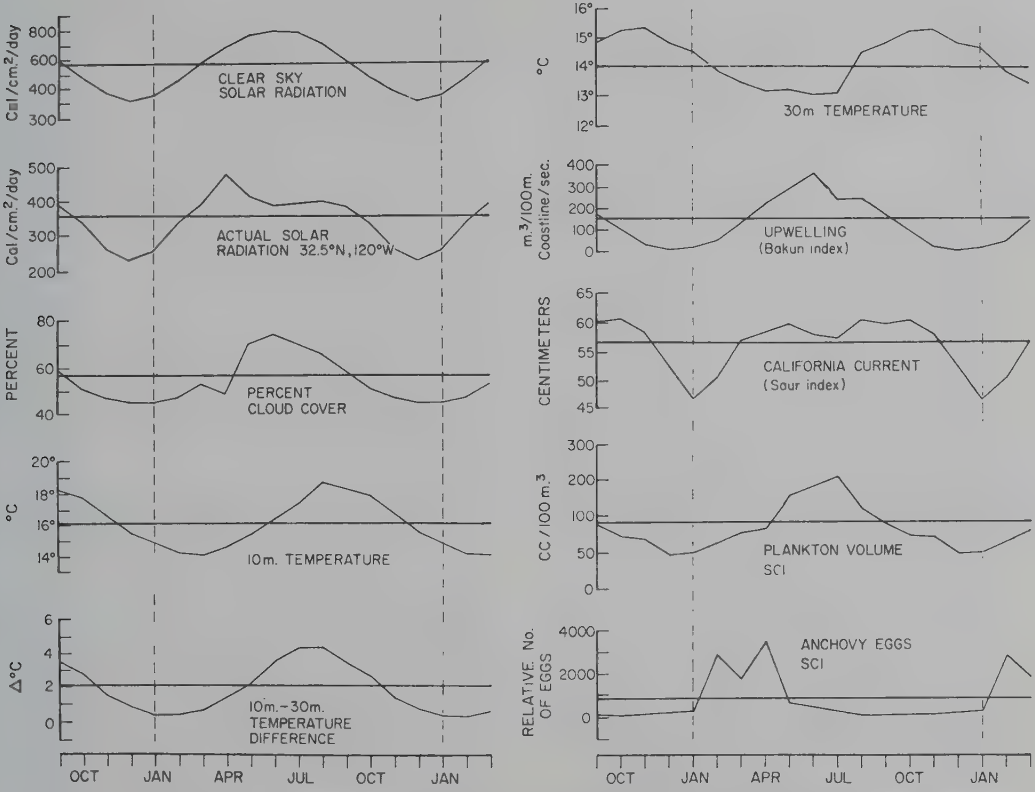

Figure 66. Seasonal cycles of solar radiation cloud cover, temperature, upwelling index, California Current strength, plankton volume and anchovy eggs from various sources and over various periods, modified from Lasker and Smith (in press).

carry the planktonic stages of larvae offshore and south of the places where spawning occurs.

ZOOPLANKTON

The plankton volume cycle indicates a mass surplus of production over consumption from December to July with a maximum rate of increase in the standing stock of zooplankton from April to May and the maximum rate of decrease from July to August. The maximum rate of increase coincides with rapidly increasing day length and elevation of the sun, while the maximum rate of decrease of the plankton would be likely to reflect continued high primary productivity with a greatly increased consumption by fishes and other consumers spawned in the spring and summer. The gradual decline in zooplankton which follows, probably indicates a declining general production rate with decreasing day length and elevation of the sun, and a decrease in upwelled nutrients: this all takes place in the continued high consumption of the spring cohorts of various consumer species.

SPAWNING

The incidence of anchovy eggs is at a maximum in February, March and April. This coincides with the maximum weight of gonads at about 6% of the mature anchovy's body weight (Fig. 66). The minimum gonad index of about 1% is attained in July and August. The maximum rate of increase in fat deposits is in the summer which probably reflects the minimum elaboration of spawning products, the maximum zooplankton standing stock as well as the maximum rate of decrease in standing stock. Anchovy produce smaller, as well as fewer, eggs in summer.

ANNUAL CHANGES

Proportionate changes from year to year in solar radiation, upwelling, and flow of the California Current appear to be relatively small, relative to seasonal changes. It appears that while the annual and seasonal averages are rather regular, there are important changes in timing and short-term maxima in upwelling. Net zooplankton display large changes in standing stock from year to year. Annual changes of 15-fold have been observed while the seasonal cycle is of the order of 5-fold or less. Spawning appears to be a simple function of the biomass of adults in the northern anchovy and the annual record reflects little more complexity than the rapid increase of anchovy over the past 25 years.

ANCHOVY MORTALITY

The major causes of larval mortality now being investigated are starvation, predation and their interrelationships. The primary interrelation appears to be that sublethal shortages of food, slow growth and development rates, leave the larvae vulnerable to predation for extended periods. Among the density-dependent forms of these mortality features are:

1) Starvation:
   a. the adults produce more larvae and juveniles than can be supported by the carrying capacity of the stock's environment.
   b. crowded adults invest eggs with deficient yolk and the resultant larvae starve at a rate which does not permit unit replacement of the spawning biomass.
   c. crowded adults are forced to spawn outside optimum areas for larval and juvenile survival and growth, or in seasons in which eggs and larvae are swept out to such areas.

2) Predation:
   a. feeding activities of adults kill so many eggs and larvae by ingestion that unit replacement of the spawning biomass is precluded; for example, crowded adult anchovy may switch from a preponderance of feeding by biting, which can be avoided by larval stages of anchovy, to feeding chiefly by filtration which cannot be avoided by the embryonic stages of anchovy.
   b. spawning rate of the stock becomes so high that population growth or aggregation of predatory species on any single stage of the anchovy life cycle increases mortality and does not permit unit replacement of the spawning biomass.

Density-independent sources of mortality such as mixing and cooling of the ocean below physiological thresholds or an influx of predators can be important as well. Predation on anchovy embryos has been measured for copepods (Lillelund and Lasker, 1971) and for euphausiids (Theilacker and Lasker, 1974) and has been observed in samples by Alvariño (1976)[1] by chaetognaths over a wider range of sizes of anchovy. Presumably, too, the filtering organisms, the abundant thaliaceans and larvaceans, and the passive paralytic predators, the coelenterates and cnidarians, are all important. This means that the anchovy larvae, always a small proportion of the plankton volume, are continuously vulnerable to a vast majority of the zooplankton organisms which are captured in the same net. It is doubtful that any of these predators depend on anchovy for a large proportion of their metabolic requirements, but the effect of their predation is part of the density independent causes of mortality for anchovy.

LABORATORY EXPERIMENTS

Basic measurements on metabolic requirements, food capture ability, and search behaviour (Hunter, 1972) of the larvae have outlined the required density and quality of food to be furnished by the environment. An early conclusion from this series of laboratory experiments was that the requirements were seldom met on the average in the anchovy spawning area. Very few systematic or quantitative samples of anchovy larval food had been taken or analysed by species in the anchovy spawning area. This led Lasker (1975) to conduct a direct larval bioassay of ocean waters in which first-feeding larvae spawned and reared in the laboratory were provided with water collected at sea to test their ability to feed. This led to the discovery of a large horizontal area which contained thin strata of dense aggregations of *Gymnodinium* and demonstrated the need for development of theory on the relationship of larval anchovy survival and growth to prey microdistribution and larval behaviour.

THEORETICAL MODELS

One theoretical model uses all the survival, growth and behaviour information available to assemble a comprehensive simulation of growth through the early larval stage (4–20 mm) for 1 or 2 months, depending on temperature (13·5°–17·5°C). A startling result of this simulation was that if the mean abundance of food was not adequate, the variance/mean ratio index[2]

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[1] Reported in monthly reports of the National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California.

[2] Several methods of describing contagion use sample parameters of variance and mean to express the significance and intensity of patchiness.

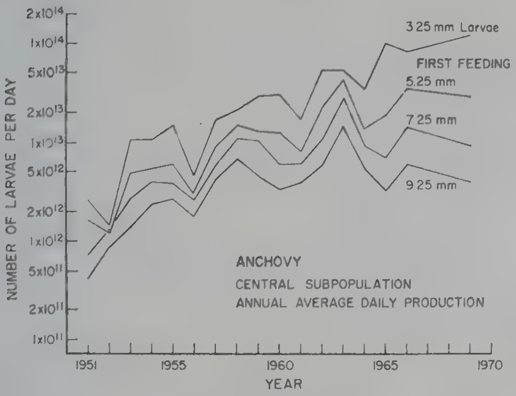

Figure 67. Time series of larval production by the central subpopulation of northern anchovy. Ordinate is expressed as the number entering the size category per day. Distance between adjacent lines is the first approximation to larval mortality within the interval. The 3·25 mm stage is a continuation of the embryonic stage following hatching since yolk persists, no functional mouth or eye has developed and feeding has not yet commenced.

of patchiness had to be above 6, was optimum at about 14, and was favourable, but declining slowly over a wide range of patchiness indices up to 1000 (Vlymen, 1977). This interesting result will allow simple multiple sampling of a site and the setting of absolute threshold criteria regarding the number of organisms ranging in size from dinoflagellates to nauplii and their distribution patterns.

Another theoretical model uses all the sized-larva collections from the sea to estimate mortality rate (Zweifel and Smith, 1976) of anchovy larvae. In general, they show that only one larva survives from a thousand anchovy eggs after a month, with a mortality of about 53% per day in the embryonic period and about 13% per day in the early larval period. This means that the stringent set of conditions set by the Vlymen model with the predation by adults of the same species, predation by all others, drift into unsuitable areas, and all other forms of mortality need to be surpassed by at least one larva from a thousand eggs after a month. In the series under consideration (1951–1969) (Fig. 67), there was no evidence of density dependence in the mortality of embryos. In the past 14 years of population increase, the early larva mortality rate averaged less than 12% per day, but at the population maximum, mortality shifted to 21% per day for the first 8 to 17 days after spawning (Fig. 68). In each year, the larval mortality rate was less than the embryonic survival rate (Fig. 69) suggesting that predation of the embryos is a regular feature of spawning and that the mortality and vision which accompanies the onset of feeding also functions to reduce drastically the overall mortality rate to an even greater extent than the food requirement is accelerating mortality.

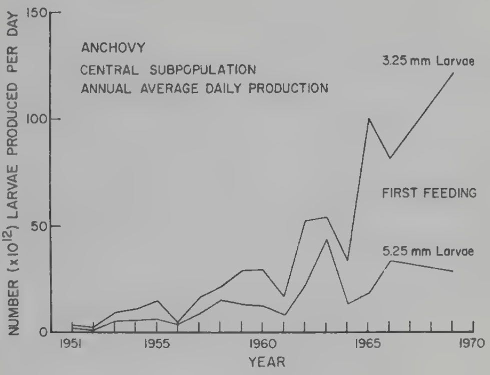

Figure 68. The time series of Figure 67 at the 3·25 mm and 5·25 mm embryo to larva transition is emphasized by plotting on the arithmetic scale rather than the logarithmic scale.

Events in the development of anchovy larvae are being examined (Hunter, 1976) for impact on the survival of larvae and for the effect on sampling. Hatching occurs at about 2·4 days at a temperature of 16·2°C. At hatching, larvae are unpigmented and have no functional eye or mouth, and are inactive

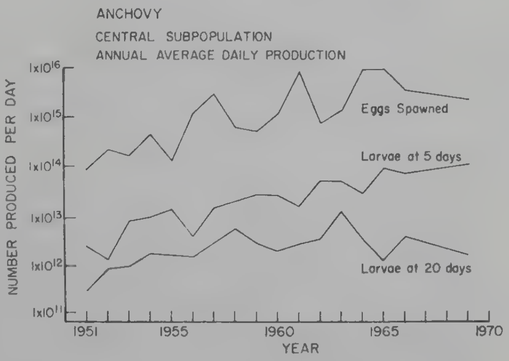

Figure 69. Back projections of spawning rate, assumed to be proportional to spawning biomass as compared with forward projections of the number of larvae near the end of the early larva phase before air bladder filling and schooling behaviour begins (adjusted for 16·2°C). A 5-days-old larva is just beginning to feed at this temperature.

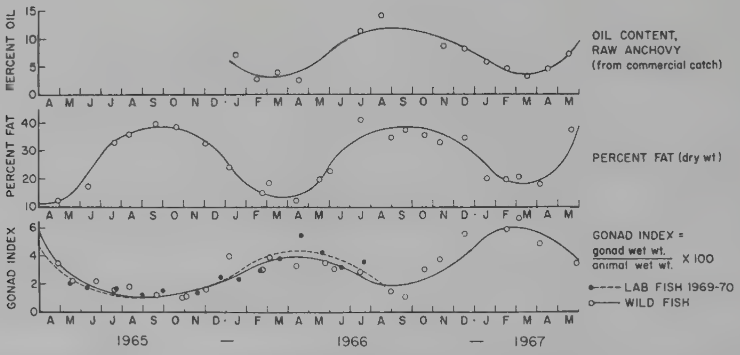

Figure 70. Annual northern anchovy central sub-population fat and gonad cycles for 1965-1967, after Lasker and Smith (in press).

90% of the time. Olfactory and lateral line organs are developed. The major activity is in short bursts of swimming which are likely to be for clearing the larval integument boundary layer of accumulated respiratory and excretory products. Between about 4·1 and 4·2 mm standard length, 7 days after spawning, yolk absorption is nearly complete, functional eyes and mouth exist and locomotor activity is increased. Larval orientation and swimming behaviour have endowed the larva with the ability to remain in patches of dense food particles. Feeding strike success begins at about 10% and increases to 90% at 23 days old. The early larval period discussed here ends with the formation of a functional hydrostatic bladder presumably for energy conservation at night (Hunter and Sanchez, 1977). In the laboratory, when no food is given, starvation is complete before nine days after spawning and total mortality occurs before 11 days. Larvae may survive the early larval period (to 23 days) on only *Gymnodinium* as food, but the larval length never exceeds 6 mm as compared with 10 mm for larvae fed phytoplankton, rotifers and crustacean nauplii.

FIELD STUDIES

Field studies on mortality to date have been totally dependent on laboratory determinations of critical rates as affected primarily by temperature. The quality of the mortality rates, then, is dependent on the comparability of the laboratory and field experiments. Laboratory descriptions of larval food requirements presently exceed, in quality, our ability to describe the feeding environment at sea. This situation is now being remedied by the development and use of pumps, closing bottles, *in situ* particle counters, and ultra-high frequency acoustic probes. The Vlymen patchiness model for larval food describes the mean abundance and variance we are looking for and hopefully one or more of the devices will be efficient enough to deploy over an 80 000 n m^2 brood area. Independent age/length tests conducted by embryonic and larval otolith daily rings are now being assembled to confirm or adjust laboratory growth and development rates for direct use in the field (Brothers et al, 1976).

ADULT PHYSIOLOGY

The primary reason for being concerned about adult anchovy physiology in the context of the larval ecosystem is that spawned eggs may not be equally capable from year to year of yielding viable embryos and larvae. It has been observed that eggs sampled in the summer are smaller than eggs sampled in the winter. This size variability raises the possibility that eggs spawned after a low productivity summer, in the following winter, might be different in the quality and quantity of yolk and the size of the hatching larvae (Hunter, in press). Were this to be predictive, the gonad condition and oil content of the early season catch could be used to regulate the fishery on adults so as to avoid low recruitment in an ensuing year. The fat cycle and the gonad cycle are inversely related and the fat cycle is related to the plankton volume cycle (Figs 66 and 70). Valdivia (1974) noted the anomalously low number of adults in the spawning stage prior to the onset of "El Niño" conditions in 1971, and this could have complicated the usual stock-recruit ratio calculation. Both the spawning rate and apparent survival of larvae was low in the El Niño period.

DISCUSSION

Laboratory experiments, theoretical models and field studies used together to study the anchovy through the embryonic and early larval stages lead to important, if tentative, conclusions: 1) larvae have the sensory and motor capacity to remain in patches of dense food and to improve the chances of locating dense food patches when outside them, 2) embryonic mortality appears to be independent of stock size over a wide range of stock sizes of the northern anchovy central sub-population, 3) early larval mortality may become stock size dependent at extremely high stock sizes.

These findings raise the need for combined biological, chemical and physical oceanographic information. We know now that we need more than the usual environmental and biological measurements and that many of the useful parameters cannot be measured efficiently over the broad areas occupied by the anchovy.

PHYSICAL OCEANOGRAPHY

The chief contribution to studies of fish survival in the larval stage in the discipline of physical oceanography is to describe the interaction of wind stress, upwelling and mixing. Pycnocline formation and destruction alternately maintains and destroys layering of larval food organisms. The maximum larval abundance appears to occur in a stable period between the one of turbulent mixing of winter storms and that of shoaling of the mixed layer by phenomena related to the upwelling cycle. We need efficient ways of estimating these effects over large areas.

CHEMICAL OCEANOGRAPHY

We need to know the time course of enrichment of the upper layers and the effect of insufficient or mistimed primary production on the fat cycle of the anchovy spawning biomass. We do not have an adequate description of the spatial and temporal effects of excretion by the major populations recycling some of the nutrients and incorporating others in growth.

BIOLOGICAL OCEANOGRAPHY

The major information in support of larval ecology that is required from biological oceanography is in the area of population dynamics of prey, of competition with and predators on anchovy larvae. Next in order of importance is a knowledge of the spatial structure of these populations on the 10's to 100's of metres scale. The coincidence of patches of larvae and their prey has been shown to be critical. The high mortality of embryonic stages may be due to the coincidence of predators in the patches of spawn modified by behaviour. Sampling programmes to describe the scale and intensity of patchiness of critical species are needed in the brood areas.

SUMMARY

A patch of anchovy larvae will have more survivors in the sea if it coincides with a succession of patches of food organisms and also if it does not coincide with a patch of effective predators. While adequate primary and secondary production are necessary to the reproductive processes of gonadal growth, egg and sperm maturation, embryonic survival and larval growth, they are not sufficient to insure larval survival. The pelagic environment must also foster and maintain discrete patterns in the distribution of larval food, the larvae and their predators. The interdisciplinary approach to the problem of understanding and regulation of fisheries in the context of variable and productive environments in upwelling areas remains to be effectively designed.

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7830

NORTHERN ANCHOVY SCHOOL SHAPES AS RELATED TO PROBLEMS IN SCHOOL SIZE ESTIMATION

JAMES L. SQUIRE, JR.[1]

ABSTRACT

Horizontal fish school profiles of the northern anchovy, *Engraulis mordax*, taken from day aerial photographs and video tapes of school bioluminescence at night were examined to determine the percentage of school area within a circular field of view and the school length and width ratios. Schools observed during the day had an average length to width ratio of 2.09:1, at night the ratio was 2.53:1. The percent coverage of the school's area in relation to a circle drawn tangent about the school averaged 42.1% during the day and 29.2% during the night. The effect of school shape on estimation of individual school area as observed with a side-looking sonar was determined. School width measurements, similar to that obtained by the sonar, were used to determine school area and indicated a possible average overestimate of the actual school area of 1.72:1. The relation of school length and width to the error was determined, indicating the greater the length to width ratio the greater the error.

Profiles of fish schools as viewed and photographed in the horizontal plane from an airborne platform have been published by numerous authors. Radakov (1972), in his review of fish schooling, described the characteristic horizontal shapes of fish schools in nature as being very diverse and extremely changeable. He stated that a spherical shape of a school is the rarest of all and also that a school's shape, size, or density is a result of the interaction between the fish and the physical and biological environment.

School shape and behavior in nature have been studied with such techniques as aerial observation, hydroacoustic measurements, and underwater observation. Each of these methods has limitations. Underwater visual observations are subject to restrictions due to illumination and restricted visibility. Aerial observation is limited in the day by water transparency, illumination, and reflectance from the water surface resulting from wind and wave action. Visual observation of school shape at night, as outlined by bioluminescent organisms, is limited to the moon's dark cycle or to periods of no moon, and is affected by water transparency and the density of bioluminescent organisms present in the water. Both day and night observations are limited by the school's proximity to the surface in relation to the factors affecting water visibility.

Hydroacoustic observations using lower frequency sounders of the type used commonly in sonar fish surveys give imprecise images of fish schools in the form of echograms that must be interpreted. Greater resolution of fish school shapes, but with limited range, can be obtained with ultrasonic scanning equipment (Voglis and Cook 1966).

All of these observation techniques may alter the environment and in many cases may result in modification of fish school behavior. Fish school behavior is affected when in close proximity to ships, submersibles, and divers, and aircraft (noise, shadow) could possibly modify the school, though this is not documented.

Surveys and research studies using variations of these three observation techniques are currently in use for direct biomass estimation of fish populations by observation of individual schools, school groups, and the internal structure of the school.

Hydroacoustic research on schooling fish is currently being conducted by the Southwest Fisheries Center (Smith 1970; Hewitt et al. 1976). Coastal, hydroacoustic surveys are conducted by the State of California (Mais 1974) to determine a relative abundance estimate of the northern anchovy, *Engraulis mordax*. These surveys are conducted during the daylight hours, as comparative tests indicate an increased probability of detection during this period (Smith 1970).

Aerial observations by commercial fish spotters, in the form of school counts and estimates of total tonnage, are being used by the Southwest

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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Fisheries Center to calculate indices of apparent abundance for several coastal species, including the northern anchovy (Squire 1972). To aid in the detection and quantification of pilchard, *Sardinops ocellata*, shoal occurrence off South Africa, Cram (1974) used an airborne, low-light-level, electron image intensifier to view the ocean's surface, detecting the bioluminescence of fish schools. During these night aerial surveys the school's horizontal surface area was interposed on the instrument's circular field of view, and running estimates of the percentage of coverage were made. These percentage estimates were then used in the computation of biomass estimates.

The intensifier used by the Sea Fisheries of South Africa has been used by the author off the southern California coast on an experimental basis. Due to the highly variable school shapes encountered, making estimates of the percentage of school coverage in the circular field of view are difficult. Experience indicated that examination of aerial color photographs and night low-level video tapes of anchovy school shapes for determination of the percentage of school coverage within a circle would be useful, particularly if in the future, surveys were to be conducted at night using this method for the development of biomass estimates for the northern anchovy and other near-surface schooling pelagic species.

In addition, an analysis of anchovy horizontal school shapes may assist hydroacoustic researchers in determining error parameters for computation of sonar biomass estimates. Hydroacoustic surveys currently conducted for the northern anchovy use both side- and vertical-looking sonar to detect and measure fish schools and school groups during the day along a predetermined survey track line. The acoustic "beam" used in these surveys varies according to the unit and is of ±5° to 10°. When detecting the school, the side-looking sonar measures the maximum dimension in one aspect of the school, either normal to or parallel to the ship's track. For the purpose of calculating horizontal area, in contrast to the aircraft's vertical view of the actual horizontal school area, the echogram school width is assumed to be elliptical (Smith 1970). Preliminary attempts at biomass estimation from sonar surveys have used the simple assumption that a series of estimates of the width of an elliptical school from random aspects will result in an unbiased estimate of school horizontal area. In a side-looking sonar the school width is measured and provides two points of reference with the orientation of these points about the school's profile being unknown. If an ellipse is fitted randomly between these two points, the resulting average area will equal a circle, a condition that was not observed in aerial photographs of anchovy schools.

METHODS

To examine the shape of northern anchovy schools as observed during day and night and to determine what percentage the school occupies of a circle tangent to two points along the school's edge and containing the school inside the circle, a circle was drawn about school profiles obtained from a series of 20 day oblique aerial color photographs (from the photographic files of the Southwest Fisheries Center) and of 20 night photographs of fish school bioluminescence. The bioluminescent anchovy school shapes were photographed from a television monitor as it projected video tapes recorded from an airborne low-light-level television camera used during anchovy resource surveys off northwestern Mexico. The night photographs were made available through the courtesy of Zapata, Inc.[2] (Zapata Fisheries), Houston, Tex. The night surveys using low-light-level television were conducted at elevations of up to 1,828 m (6,000 ft) and this survey technique is effective because the northern anchovy commonly migrates to the near-surface area during hours of darkness (Squire 1972).

The actual area of the schools observed in the photographs are unknown due to lack of data on the aircraft's altitude, camera angle, and camera geometry; however, all were taken from angles approaching vertical. However, all area calculations are expressed in percentages of a circle drawn tangent about the school's edge.

The day school profiles were further analyzed to determine what the school area would be if the width measurement were considered to be equal to the school's diameter and what the area would be if viewed systematically from six points 30° arc) about an arc of 180° around the school (based on school width or diameter as determined similar to the measurements made from a hydroacoustic sounder). These area data calculated from the six points of observation to determine school width were then compared to the actual school area.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

School length to width ratios were determined for both day and night schools.

The school area, as expressed in terms of percentage of the circle drawn about it, was determined by tracing the school profile upon paper, cutting the school out of the circle and weighing both the school profile and the nonschool portion of the circle on a sensitive laboratory balance. School areas for the six points of school width (diameter) measurement about the 180° arc were computed statistically.

RESULTS

Night Observations

Figure 1 illustrates the profiles of schools recorded by the airborne low-light-level television system. On each figure are given the area percentage of a tangent circle that the fish school occupies and the length to width ratio.

The average percent coverage of a night anchovy school, in relation to the circle tangent to the school, is 29.2%. The average ratio of school length to width is 2.53:1.

Day Observations

Figure 2 illustrates profiles of schools observed during the day. On each figure are given the percentage of a circle tangent to the school that is occupied by the fish school, the length to width ratio, and the 30° arc points that were used to determine the school's estimated diameter and area, simulated as randomly viewed by a side-looking sonar. The ratio of the actual school area to the calculated area of the school's average, high and low estimate, as viewed every 30° of a 180° arc based on simulated sonar measurements of width, is given in Table 1.

TABLE 1.—Ratio of the actual anchovy school area to the average area based on six points of observation as viewed every 30° of a 180° area, and the high and low ratio.

School	Average	High	Low
1D	1 2 61	1.3 95	1 0 83
2D	1 1 96	1·2 91	1.0 90
3D	1 1 22	1 1 56	1 0 85
4D	1 2.12	1·3 71	1 0 63
5D	1 1 13	1 1 41	1 0 80
6D	1 2 73	1 4 53	1·1 18
7D	1 1 50	1 2 35	1 0 60
8D	1 1 32	1·2 00	1 0 54
9D	1 1.49	1 1 88	1 1 19
10D	1 1 31	1 1 60	1 1 04
11D	1 2 65	1 4 82	1 0 62
12D	1.1 33	1.2 02	1 0 85
13D	1 1 47	1 2 35	1·0 77
14D	1 1 68	1 2 54	1·0 49
15D	1 1 97	1.3 30	1 0.65
16D	1 1 60	1.2 69	1 0 44
17D	1 1.38	1·2 10	1 0 84
18D	1 1 38	1 2 00	1 0 68
19D	1 1 99	1 3 52	1.0 42
20D	1·1 77	1:2 90	1 0 66

The average percent coverage of a day anchovy school to the tangent circle about the school is 42.1%. The average length to width ratio for all day schools is 2.09:1. The ratio of estimate of the area of all day schools, as calculated from measurements from 30° arc points about the school, to the actual area of the school is 1.72:1. The ratios, length to width, and estimate of school area to actual school area were compared and Figure 3 graphs the relationship. The graph displays the variables plotted on log-log paper showing two main points: One, that the variance is changing proportionally to the mean. This is expected as there should be more variation as the school length to width increases. Two, the plotted regression line indicates that more bias (higher estimated actual school ratio) is introduced as the school length to width ratio increases. The line is significant at the 95% confidence interval as proven by the t-test ($1.98 < 2.298$). The confidence limits are from 0.0545 to 0.734.

SUMMARY AND COMMENTS

The data on day/night school length to width ratios support what is commonly known about the schooling shapes of the northern anchovy. They are more common in the near-surface area at night, generally in large elongate thin surface schools. These elongate schools tend to group together in the early morning hours and descend to depth to form more compact schools during the day (Mais 1974). Studies by Squire (1972) of aerial fish spotter data show anchovy schools to be more frequently observed, and observed in larger quantities at night, when compared with day observations.

The schools percent area coverage of the tangent circle at night is 12.9% less than its coverage during the day and the length to width ratio is greater by 0.44. In addition, analysis of school length to width ratios compared to the ratio of estimated school size to actual size (Figure 3) shows that as the length to width ratio increases a greater error in school area estimate will occur. Schools with a length to width ratio of 2:1 have an estimated to actual error of about 1.5:1 while more elongate schools of a ratio of 3:1 have an estimated error of about 1.75:1.

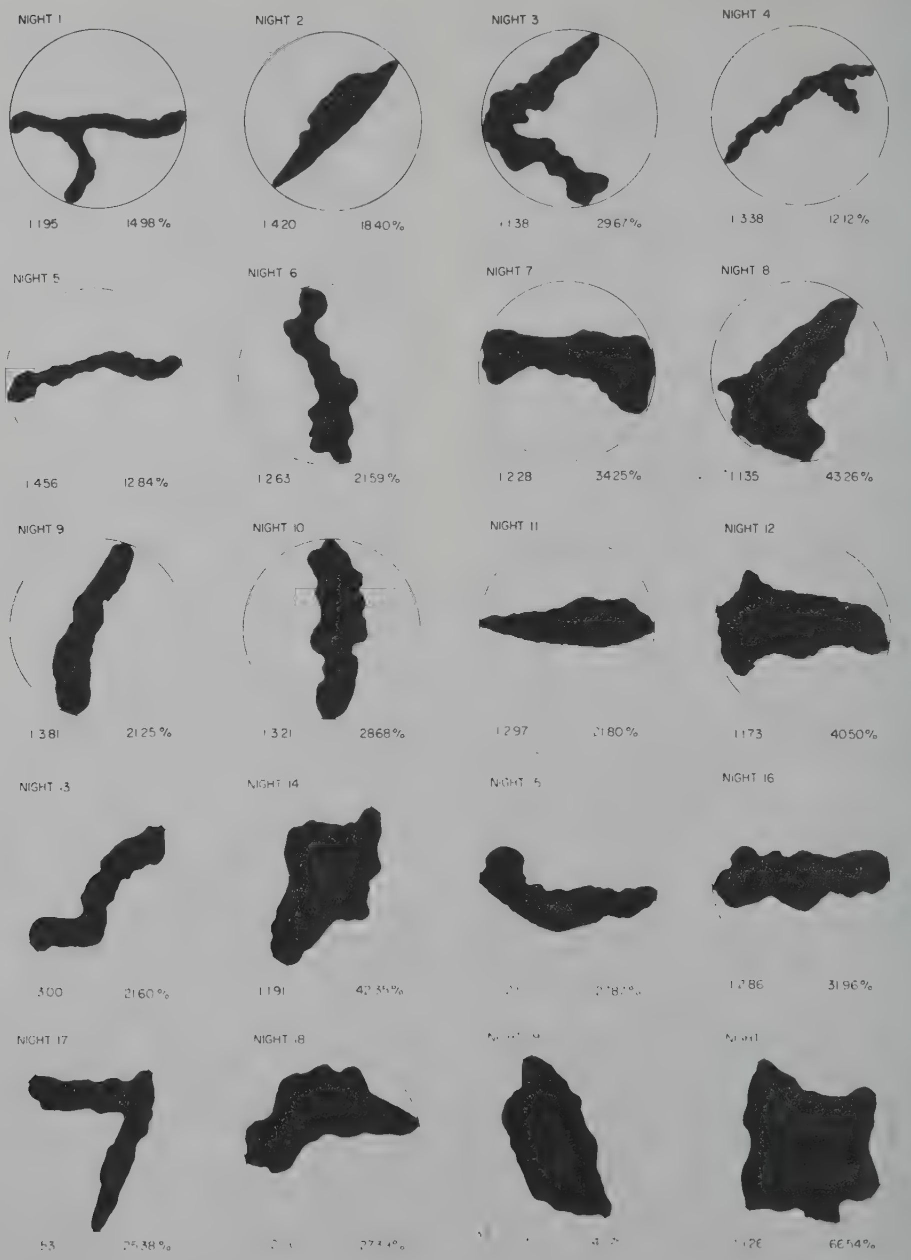
NIGHT 1
1 195
14 98 %
NIGHT 2
1 420
18 40 %
NIGHT 3
1 138
29 67 %
NIGHT 4
1 338
12 12 %
NIGHT 5
1 456
12 84 %
NIGHT 6
1 263
21 59 %
NIGHT 7
1 228
34 25 %
NIGHT 8
1 135
43 26 %
NIGHT 9
1 381
21 25 %
NIGHT 10
1 321
28 68 %
NIGHT 11
1 297
21 80 %
NIGHT 12
1 173
40 50 %
NIGHT 13
300
21 60 %
NIGHT 14
1 191
42 35 %
NIGHT 15
NIGHT 16
1 286
31 96 %
NIGHT 17
53
25 38 %
NIGHT 18
27 34 %
NIGHT
1 126
66 54 %

FIGURE 1.—Profiles of anchovy schools observed at night off southern California, indicating the width to length ratio and the percentage of a tangent circle about the school.

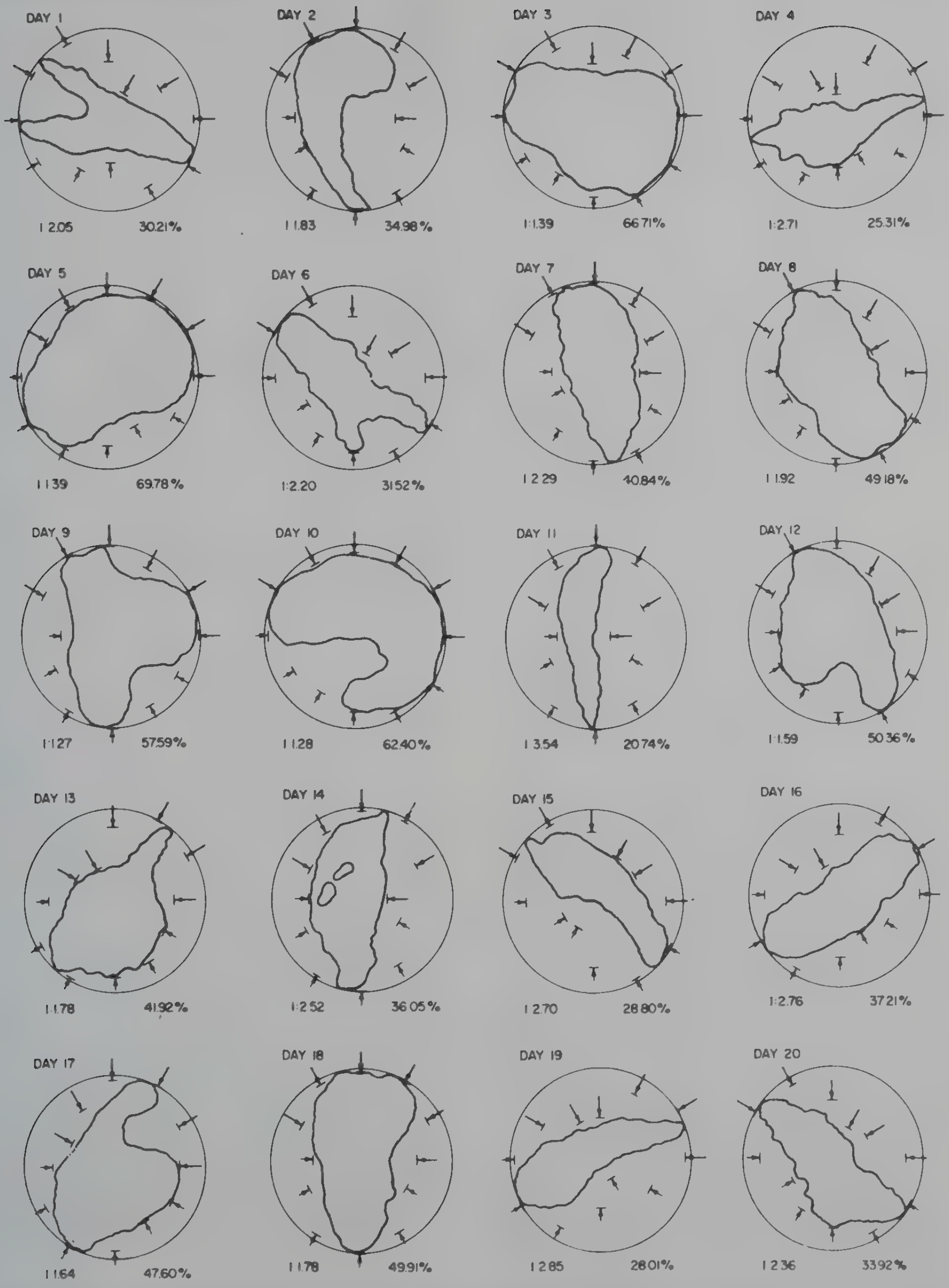
DAY 1
1:2.05
30.21%
DAY 2
1:1.83
34.98%
DAY 3
1:1.39
66.71%
DAY 4
1:2.71
25.31%
DAY 5
1:1.39
69.78%
DAY 6
1:2.20
31.52%
DAY 7
1:2.29
40.84%
DAY 8
1:1.92
49.18%
DAY 9
1:1.27
57.59%
DAY 10
1:1.28
62.40%
DAY 11
1:3.54
20.74%
DAY 12
1:1.59
50.36%
DAY 13
1:1.78
41.92%
DAY 14
1:2.52
36.05%
DAY 15
1:2.70
28.80%
DAY 16
1:2.76
37.21%
DAY 17
1:1.64
47.60%
DAY 18
1:1.78
49.91%
DAY 19
1:2.85
28.01%
DAY 20
1:2.36
33.92%

FIGURE 2.—Profiles of anchovy schools observed during the day off southern California, indicating the width to length ratio and the percentage of a tangent circle about the school. Measurements of school width were taken at the six points (long arrow shafts) indicated about a 180° arc.

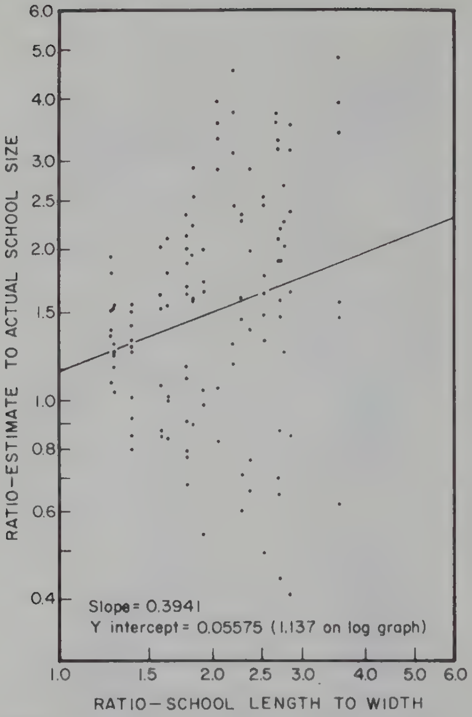

FIGURE 3.—Regression plot for the ratio estimated anchovy school size to actual size compared with the school length to width ratio.

For simulated sonar observations of school widths used in the calculation of school area, the preliminary examination of these data indicates a possible 1.72:1 average overestimate of area due to school shape deviations from a circle or ellipse.

Fish schools, being highly variable in horizontal profile, are probably equally complex in vertical structure; the relationship of horizontal complexity to vertical complexity is not known. Also unknown is the question of whether the individual school's axis is oriented in the same general direction within a group of schools, a possible factor which, if it occurs, could provide a source of substantially higher or lower school area error estimates from sonar track line surveys.

The problem of accurately estimating the percentage of school area within view of a low-light-level viewer is difficult, as the examples of school shapes within the target circle would indicate. Parameters of human viewing error could be established for this survey technique. However, the conduct of surveys using a low-light-level television system where the video signal can be recorded and later electronically analyzed with the aid of an image analyzer, should result in a higher degree of survey accuracy.

School shapes were taken from photographs randomly selected from an aerial photo file. Many of the photos were taken in the nearshore areas. There is the possibility that schools may be slightly more elliptical in shape over deep water than in the nearshore areas, but this is not documented. If this were true the error estimate would be reduced. This and other aspects of school profile and orientation should be investigated further and estimates of length to width ratios from aerial surveys, done in conjunction with each acoustic survey, may be useful for determination of a correction factor for the acoustic data.

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7831

Sea Surface Temperature Distributions Obtained Off San Diego, California, Using an Airborne Infrared Radiometer

JAMES L. SQUIRE, JR.[1]

ABSTRACT

Sea surface temperature surveys were conducted weekly off San Diego, Calif., using an airborne infrared radiometer during the months of April through October 1972-74. A total of 90 surveys were made over the 320-mile flight track. The analog chart record of temperature was keyed to a "ground truth" temperature measurement and read to determine 1 min average temperatures which were plotted on the flight track and 1°F (0.56°C) isotherms were contoured from the data. The trend of sea surface temperatures during the 3-yr period showed warmer temperatures in 1972, which was an "El Niño" year, cooler in 1973, warmer than 1973 in 1974, but not as warm as 1972. In early July 1974, an anomalous warming period occurred and highest average temperatures of 73°F (22.7°C) were recorded in 19 July 1974. Lowest average temperature of 54°F (12.2°C) was recorded on 2 April 1973.

The 1972-74 survey temperatures taken over the "ground truth" calibration site were compared with a time series of temperature observations taken during the same months from 1963 to 1968. The average temperature during 1963-68 was 63.4°F (17.4°C) and for 1972-74, 64.1°F (17.8°C), a difference of less than 1°F (0.56°C). Average monthly temperature differences, 1963-68 compared with 1972-74, shows April the same, warmer 2°F (1.12°C) for May, 3°F (1.68°C) for June, 1°F (0.56°C) for July, same for August, 1°F (0.56°C) less for September, and 2°F (1.12°C) less for October.

INTRODUCTION

Synoptic sea surface temperature surveys with an airborne infrared radiometer were first conducted off the Pacific coast in August 1963 over the coastal waters of Washington, Oregon, and California by the National Marine Fisheries Service's (NMFS) Tiburon Fisheries Laboratory at Tiburon, Calif. Surveys over three areas were conducted in cooperation with the U.S. Coast Guard, and these surveys are being continued as part of the U.S. Coast Guard oceanographic program. The first 5 yr of surveys (1963-68) were reviewed by the author (Squire 1971). The objective of the coastal program was to increase the general knowledge about the nearshore temperature structure, to define areas of nearshore upwelling, and to develop temperature data that may be useful in relating the distribution and relative abundance of major coastal species of fishes to sea surface temperature and its changes.

The initial surveys, conducted monthly, were broad in geographical scope and in time. The data have been useful in computing average catch temperatures for salmon off central California, and for a number of pelagic species common to southern California waters (Squire unpubl. manuscr.). However, this broad-based survey did not cover some of the more important coastal fishing areas in sufficient detail and at short enough time intervals to permit the determination of the relation of changes in catch composition and catch rates to short-term temperature fluctuations.

To determine short-term temperature effects, an area having a heavy amount of fishing effort and catch was selected for detailed study. This area covered the southern California coastal waters from near Del Mar, Calif., to south of the United States-Mexico border, and to about 22.3 km (12 n.mi.) offshore. The area, known by the project name of "San Diego Test Area" encompasses the major sportfishing grounds off La Jolla, Point Loma, and about the Coronado Islands off Mexico.

The airborne temperature surveys used a "ladder-type" search pattern, modified to accommodate navigational aids. These surveys were flown once each week, 1 April through 31 October during 1972 to 1974. A total of 90 surveys was made, each requiring about 2 h to complete.

OPERATIONAL PROCEDURES

The airborne sea surface temperature sensing unit used in the study was a Barnes research radiometer (PRT-5) modified with a special lens filter system to restrict the viewing range in the infrared spectrum to 10.5 to 12.5 nm. This spectral range approximates the infrared range that is used in the ITOS (NOAA, National Environmental Satellite Service) series weather satellite.

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

The PRT-5 was piloted by the author in a NMFS twin-engine aircraft over the survey flight track (Fig. 1) at elevations between 152 and 304 m (500 and 1,000 ft). Low stratus bases at 243 and 304 m (800 to 1,000 ft) common to the coastal areas were encountered on most flights during the 3-yr period. On numerous occasions, flights were rescheduled due to very low stratus or fog conditions. Only on rare occasions was there an absence of haze or low stratus, middle and high clouds, the type of conditions that would allow direct comparison of satellite data with the low altitude temperature surveys.

Calibration measurements, or "ground truth," were obtained from surface sources for each flight either from observations taken at the end of the Scripps Institution of Oceanography pier, La Jolla, Calif., or from the U.S. Naval Undersea Center's (NUC) oceanographic tower located approximately 2.8 km (1½ n.mi.) off Mission Beach, San Diego, Calif. Most comparative observations were taken over the oceanographic tower as it is located offshore, and the temperature of surrounding surface waters are relatively stable when compared with those near the outer surf zone at Scripps pier. Simultaneous sea surface temperature observations were made with either a surface bucket thermometer off Scripps pier, or a surface thermistor temperature reading from the NUC oceanographic tower. To obtain a comparative reading, the aircraft was flown over the pier or tower at an elevation of about 45.7 m (150 ft). At the moment the aircraft passed over the pier or tower, the radiative surface of the structures, being much warmer than the sea surface, would produce a response from the infrared detector to make a synchronous mark on the temperature analog recorder chart. The analog recorder chart was driven at a speed of 2.54 cm (1 in) per minute.

The temperature analog chart was keyed to the "ground truth" temperature measurement, and the chart was read to determine a 1-min average temperature, with a slide rule averaging readout device developed by the author (Squire 1971). The 1-min temperature averages were plotted on the flight track, and 1°F (0.56°C) isotherms were contoured from the data. The weekly isotherm charts were given limited distribution to a list of interested fishing and scientific organizations and their personnel.

Isotherm charts are shown in the Appendix for all surveys in 1972, 1973, and 1974 (1972, Figs. 1-28; 1973, Figs. 29-61; 1974, Figs. 62-90). For conversion of °F to °C see comparative temperature data on each figure.

RESULTS

Isotherm charts were developed for each of the 90 survey flights. Distribution of survey flight effort by month for the 3-yr period is as follows:

Month	*Flights*
April	12
May	13
June	10
July	15
August	14
September	12
October	14

June has the least number (10) of flights during the survey period, reflecting the problems of conducting aerial surveys during a period when persistent low stratus is most present over the coastal waters off San Diego.

The general trend of sea surface temperature during the 3-yr period showed that 1973 was cooler than 1972, which was an "El Niño" year with above-normal warming along the west coast of North and South America (Miller and Laurs 1975). Temperatures in 1974 were warmer than those observed in 1973, but not as warm as those experienced in 1972. However, in 1974, an anomalous warming period occurred in early July off southern California, and the highest temperatures were recorded at that time. Examples of isotherm patterns observed during surveys having the lowest average temperature (2 April 1973) and the highest average temperature (19 July 1974) are shown in the Appendix, Figures 31 and 76.

Semimonthly isotherm charts of the northeastern Pacific, developed from ship data, are issued by the NMFS Southwest Fisheries Center. To develop data for comparative purposes, weekly temperatures were then averaged by semimonthly periods for each month, 1 through 15 days and 16 through 30/31 days, for the 3 yr of data from temperatures observed at locations along the survey flight track, as shown in Figure 1. Isotherm charts in 1°F with °C equivalents drawn to these semimonthly data are presented in Figures 2 to 15.

The only time series of infrared sea surface temperature data available for comparison with the 1972 to 1974 data off San Diego is the 1963-68 data resulting from the cooperative program with the U.S. Coast Guard. During these surveys, ground truth calibration checks were also made over the NUC oceanographic tower. Comparing 1963-68 monthly average temperatures (to the nearest whole °F) for the area off Mission Beach (NUC tower area) with those observed in the same location during the 1972-74 surveys, we note an average difference of less than 1°F (0.56°C). The average temperature for 1963-68 was 63.4°F (17.4°C) and for 1972-74 was 64.1°F (17.8°C). Average monthly temperatures rounded to the nearest °F for the 3-yr period were observed (Table 1) to be the same for April, warmer 2°F (1.12°C) for May, 3°F (1.68°C) for June, 1°F (0.56°C) for July, the same for August, 1°F (0.56°C) less for September, and 2°F (1.12°C) less for October.

A general description of sea surface temperature patterns that would be typical of those usually observed off San Diego during the weekly surveys is as follows: Temperatures that are greater than any other locations in the survey area are usually found north offshore and to the northwest of La Jolla. From off La Jolla Point to Pacific Beach and continuing southwest and offshore to the southwest is an area of upwelling with generally lower temperatures than those to the north. Evidences of this

Table 1.—Comparative temperatures—U.S. Naval Undersea Oceanographic Tower for airborne infrared sea surface temperature surveys, 1963-68/1972-74.

Month	1972-74 monthly mean temperature °C	1972-74 monthly mean temperature °F	1963-68 monthly mean temperature °C	1963-68 monthly mean temperature °F
April	14.6	58.2	14.4	58.0
May	16.8	62.3	15.6	60.0
June	18.4	65.3	16.7	62.0
July	19.7	67.4	18.9	66.0
August	20.0	68.0	20.0	68.0
September	17.3	63.3	18.3	65.0
October	17.3	63.3	18.3	65.0

upwelling area was also observed when a temperature decline, sometimes sharp, was frequently present west of Mission Beach and the NUC tower when proceeding toward the coast. The kelp bed area west of Point Loma appears to be slightly warmer than the area to the north off Mission Beach. Near the area south of Point Loma and about the San Diego harbor entrance channel, a significant drop in temperature is usually observed, this resulting from upwelling near the south end of the Point. Temperatures tend to remain lower than those found west of the Point Loma peninsula and they remain lower to the southeast of Point Loma, off the Coronado Strand, and increase slightly off Imperial Beach. Immediately south of the International Border of Mexico is frequently found the northern edge of an extensive coastal upwelling zone. The effects of this upwelling increase to the south and extend further offshore. Warmer temperatures than those found near the coast of Mexico are encountered offshore about the Coronado Islands, and temperatures in this area are more typical of those found offshore in the northern portion of the survey area.

ACKNOWLEDGMENTS

The interest and cooperation of E. C. LeFond, Dale Good, Paul Hansen, and the staff associated with the NUC oceanographic tower in making sea surface calibration observations is appreciated. To a number of personnel from the Southwest Fisheries Center, NMFS, NOAA, and to Clyde Melendy of the National Weather Service, NOAA, who took time from their activities to assist in the airborne surveys, I express my appreciation.

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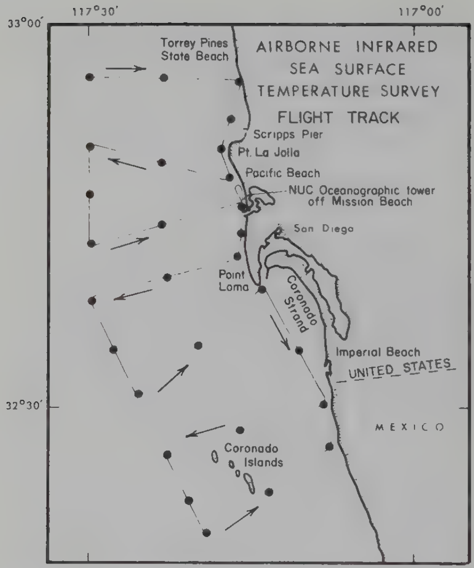
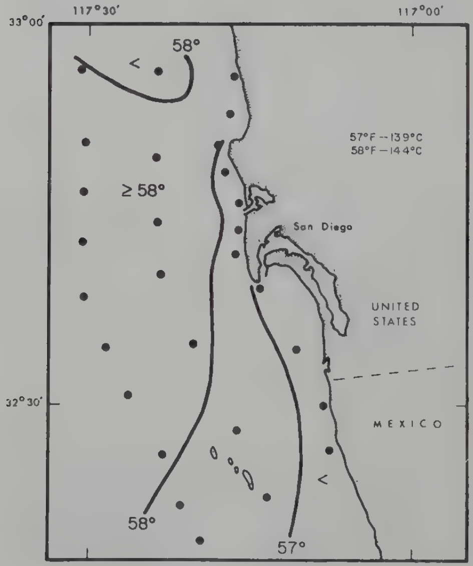

117°30'
117°00'
33°00'
32°30'
AIRBORNE INFRARED SEA SURFACE TEMPERATURE SURVEY FLIGHT TRACK
Torrey Pines State Beach
Scripps Pier
Pt. La Jolla
Pacific Beach
NUC Oceanographic tower off Mission Beach
San Diego
Point Loma
Coronado Strand
Imperial Beach
UNITED STATES
MEXICO
Coronado Islands

Figure 1.—Survey flight track pattern flown during the 3-yr study. Dots indicate points where temperatures were taken for the development of biweekly average isotherm charts.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117°00'
33°00'
32°30'
58°
<
57°F – 13.9°C
58°F – 14.4°C
≥ 58°
San Diego
UNITED STATES
MEXICO
<
58°
57°

Figure 2.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 1 to 15 April 1972-74.

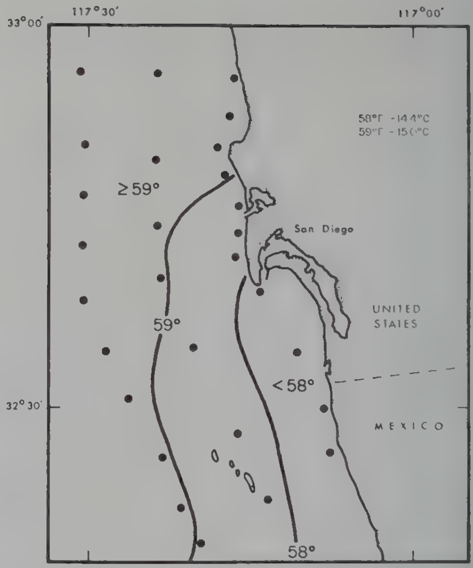

117°30'
117°00'
33°00'
32°30'
58°F - 14.4°C
59°F - 15.0°C
≥ 59°
San Diego
59°
UNITED STATES
< 58°
MEXICO
58°

Figure 3.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 16 to 30 April 1972-74.

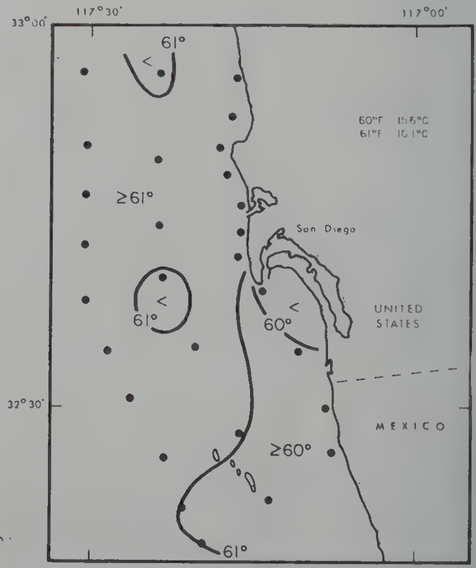

117°30'
117°00'
33°00'
32°30'
61°
<
60°F 15.6°C
61°F 16.1°C
≥61°
San Diego
<
61°
<
60°
UNITED STATES
MEXICO
≥60°
61°

Figure 4.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 1 to 15 May 1972-74.

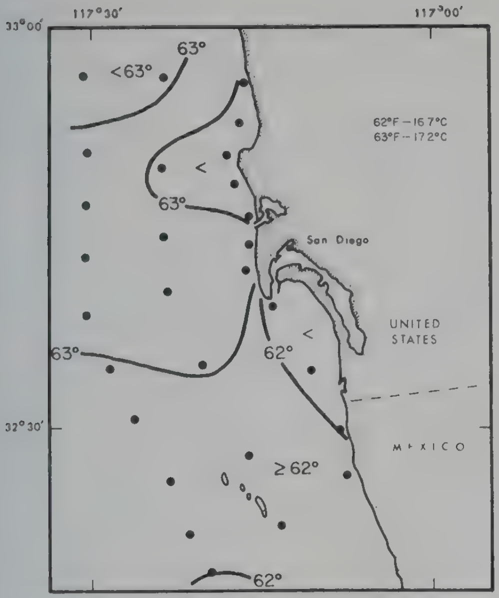

117°30′
117°00′
33°00′
32°30′
63°
<63°
62°F – 16.7°C
63°F – 17.2°C
<
63°
San Diego
UNITED STATES
63°
62°
<
MEXICO
≥62°
62°

Figure 5.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 16 to 31 May 1972-74.

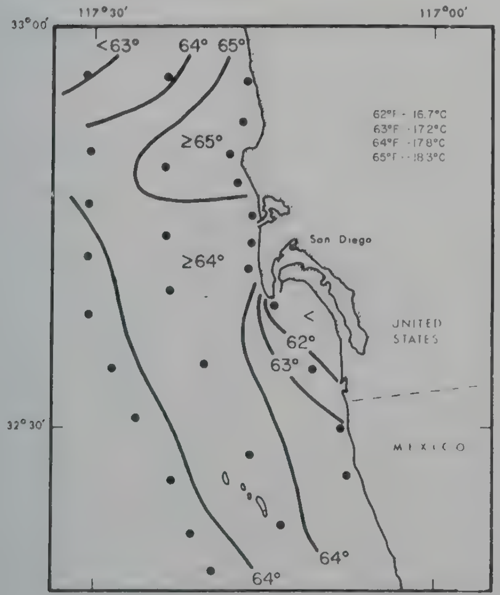

117°30′
117°00′
33°00′
32°30′
<63°
64°
65°
62°F – 16.7°C
63°F – 17.2°C
64°F – 17.8°C
65°F – 18.3°C
≥65°
San Diego
≥64°
<
UNITED STATES
62°
63°
MEXICO
64°
64°

Figure 6.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 1 to 15 June 1972-74.

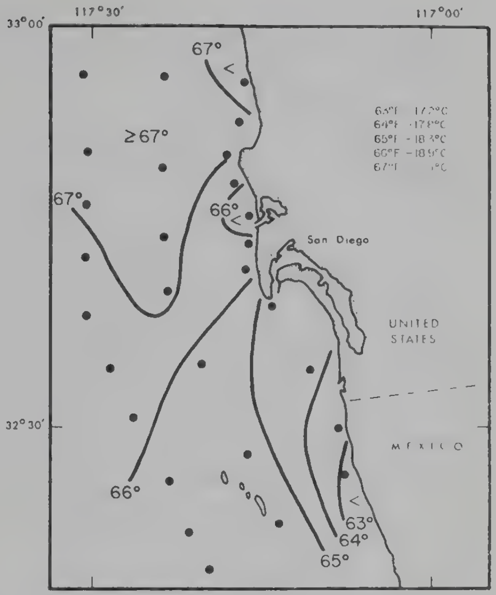

117°30′
117°00′
33°00′
32°30′
67°
<
64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
≥67°
67°
66°
<
San Diego
UNITED STATES
MEXICO
66°
<
63°
64°
65°

Figure 7.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 16 to 30 June 1972-74.

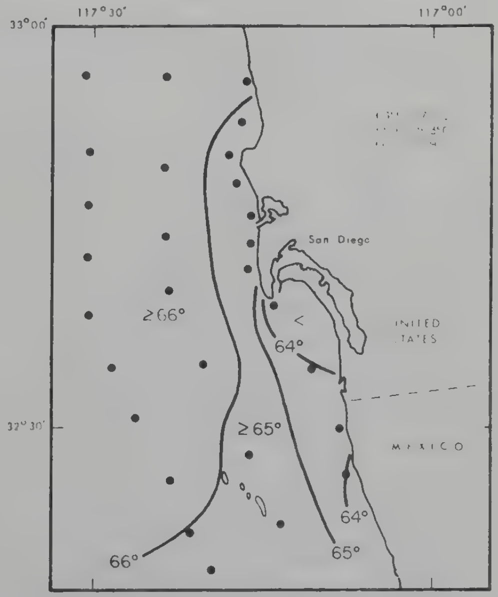

117°30′
117°00′
33°00′
32°30′
San Diego
≥66°
<
UNITED STATES
64°
≥65°
MEXICO
64°
66°
65°

Figure 8.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 1 to 15 July 1972-74.

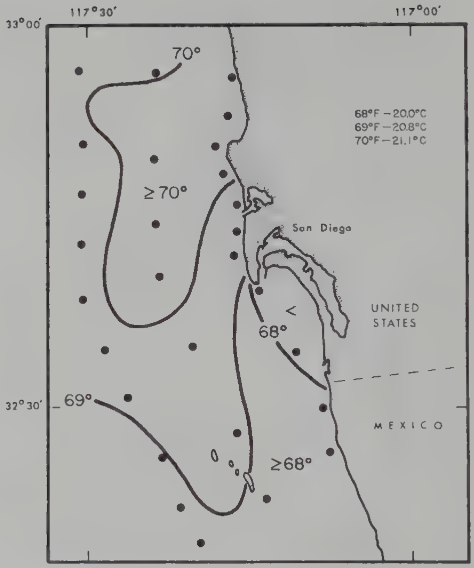

33°00′
117°30′
117°00′
70°
68°F — 20.0°C
69°F — 20.8°C
70°F — 21.1°C
≥ 70°
San Diego
UNITED STATES
<
68°
32°30′
69°
MEXICO
≥68°

Figure 9.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 16 to 31 July 1972-74.

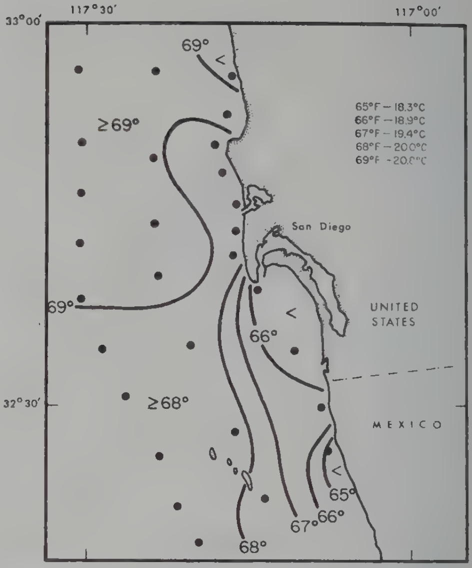

33°00′
117°30′
117°00′
69°
<
≥69°
65°F — 18.3°C
66°F — 18.9°C
67°F — 19.4°C
68°F — 20.0°C
69°F — 20.8°C
San Diego
69°
UNITED STATES
<
66°
32°30′
≥68°
MEXICO
<
65°
67°
66°
68°

Figure 11.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 16 to 31 August 1972-74.

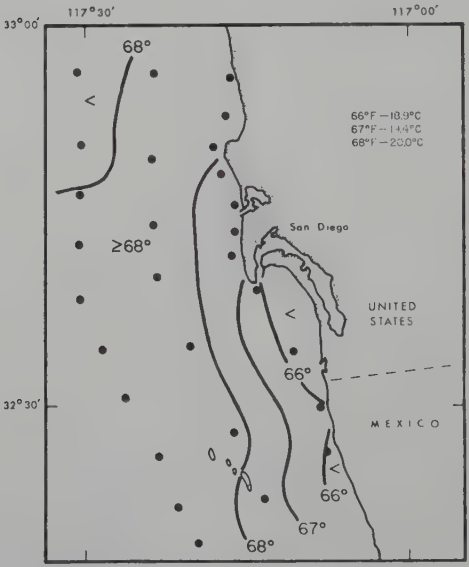

33°00′
117°30′
117°00′
68°
<
66°F — 18.9°C
67°F — 19.4°C
68°F — 20.0°C
San Diego
≥68°
UNITED STATES
<
66°
32°30′
MEXICO
<
66°
67°
68°

Figure 10.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 1 to 15 August 1972-74.

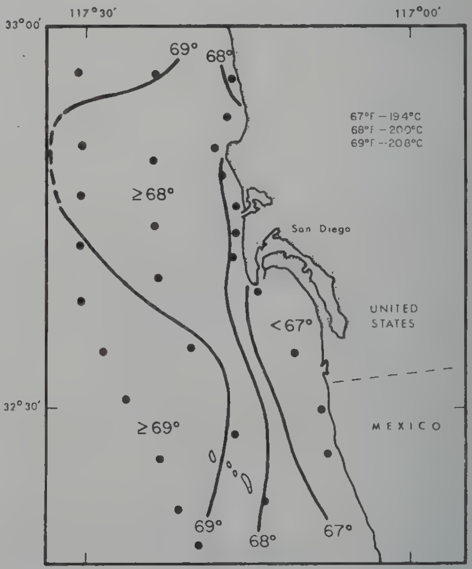

33°00′
117°30′
117°00′
69°
68°
67°F — 19.4°C
68°F — 20.0°C
69°F — 20.8°C
≥68°
San Diego
UNITED STATES
<67°
32°30′
≥69°
MEXICO
69°
68°
67°

Figure 12.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 1 to 15 September 1972-74.

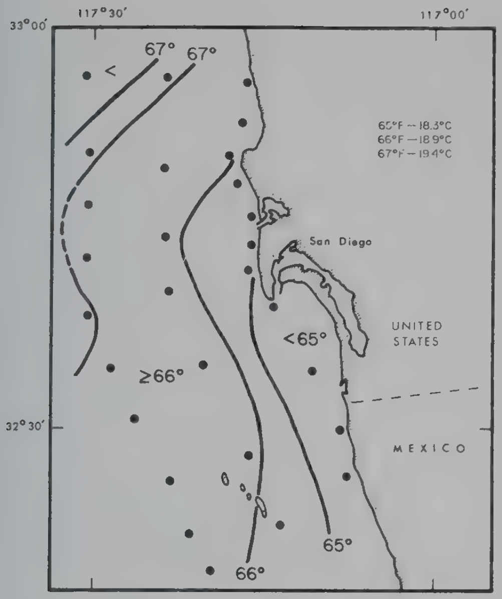

117°30′
117°00′
33°00′
32°30′
67°
67°
<
65°F – 18.3°C
66°F – 18.9°C
67°F – 19.4°C
San Diego
≥66°
<65°
UNITED STATES
MEXICO
66°
65°

Figure 13.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 16 to 30 Septembver 1972-74.

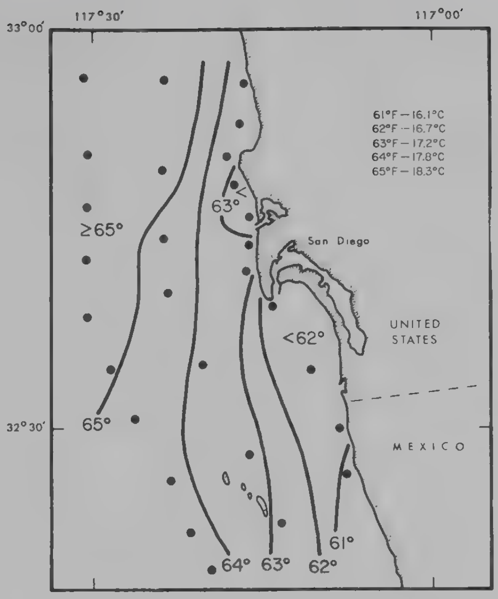

117°30′
117°00′
33°00′
32°30′
61°F – 16.1°C
62°F – 16.7°C
63°F – 17.2°C
64°F – 17.8°C
65°F – 18.3°C
≥65°
63°
<
San Diego
<62°
UNITED STATES
MEXICO
65°
61°
64°
63°
62°

Figure 15.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 16 to 31 October 1972-74.

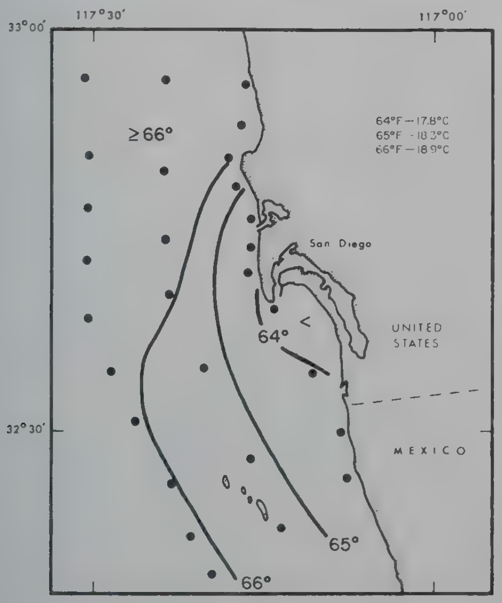
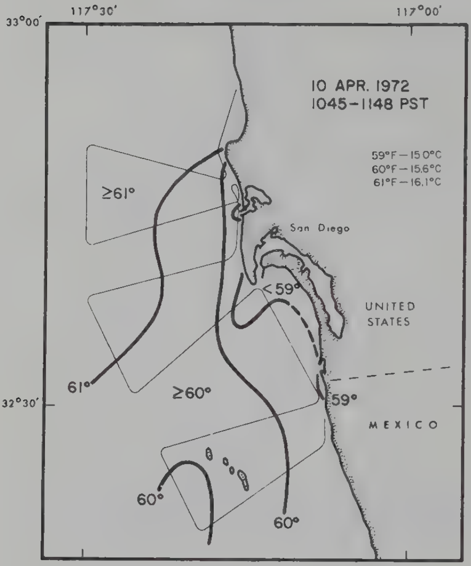

117°30′
117°00′
33°00′
32°30′
≥66°
64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
San Diego
64°
<
UNITED STATES
MEXICO
65°
66°

Figure 14.—Average isotherm patterns observed off San Diego in °F with °C equivalents for the 3-yr period, 1 to 15 October 1972-74.

APPENDIX

Sea surface temperature isotherms observed during survey flights off San Diego. Figure 1 to 90.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117°00′
33°00′
32°30′
10 APR. 1972
1045–1148 PST
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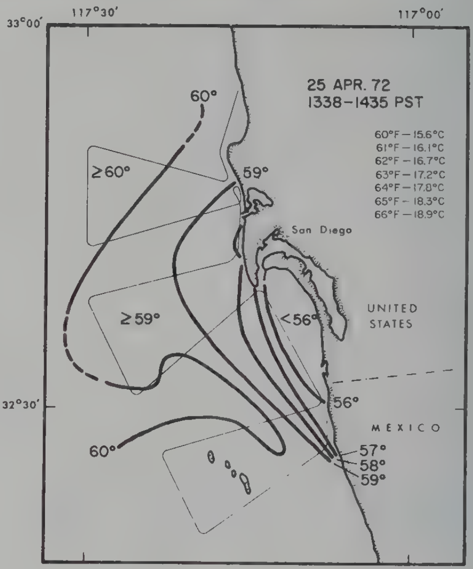
60°F – 15.6°C
61°F – 16.1°C
≥61°
San Diego
<59°
UNITED STATES
61°
≥60°
59°
MEXICO
60°
60°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33°00′
32°30′
25 APR. 72
1338–1435 PST
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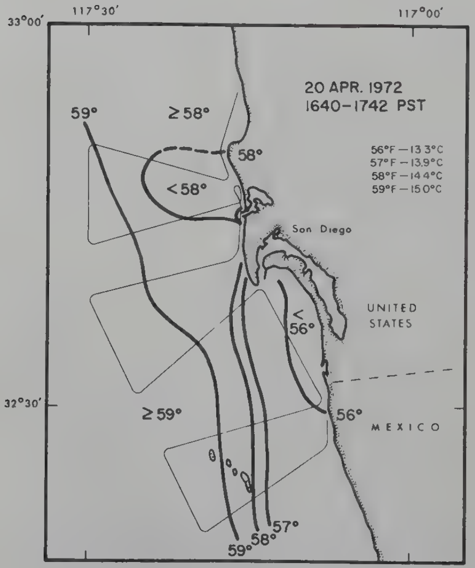
62°F – 16.7°C
63°F – 17.2°C
64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
≥60°
59°
San Diego
≥59°
<56°
UNITED STATES
56°
MEXICO
60°
57°
58°
59°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117°00′
33°00′
32°30′
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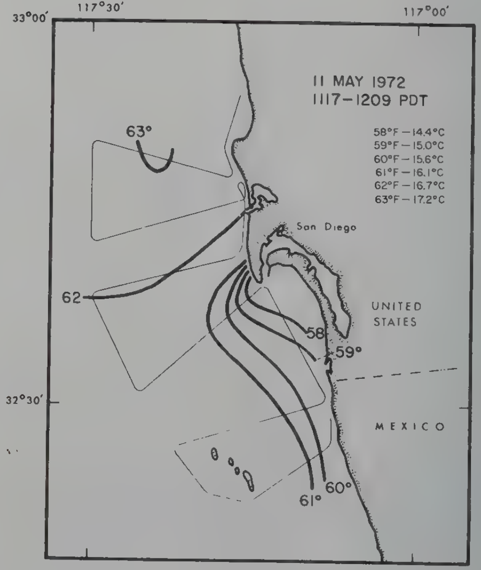
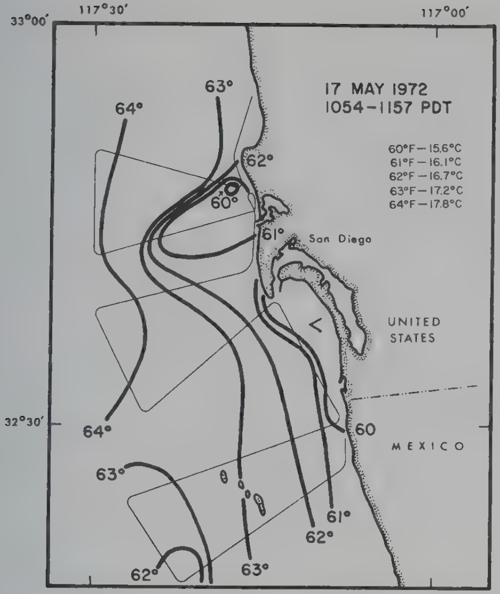
1640–1742 PST
59°
≥58°
58°
56°F – 13.3°C
57°F – 13.9°C
58°F – 14.4°C
59°F – 15.0°C
<58°
San Diego
<56°
UNITED STATES
≥59°
56°
MEXICO
57°
58°
59°


117°30′
117°00′
33°00′
32°30′
11 MAY 1972
1117–1209 PDT
63°
58°F – 14.4°C
59°F – 15.0°C
60°F – 15.6°C
61°F – 16.1°C
62°F – 16.7°C
63°F – 17.2°C
San Diego
62
UNITED STATES
58
59°
MEXICO
61°
60°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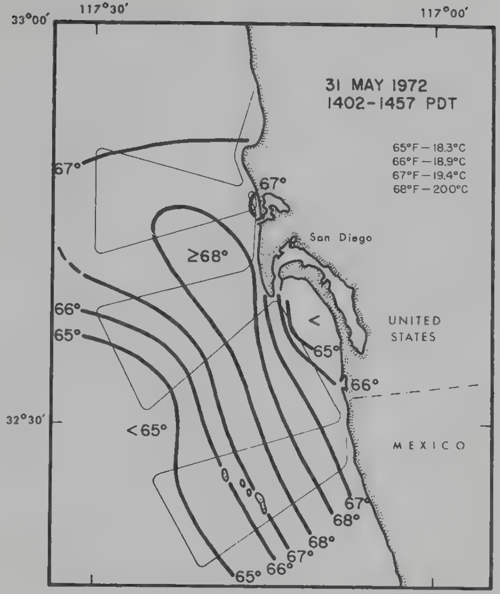
117°30′
117°00′
32°30′
17 MAY 1972
1054–1157 PDT
60°F — 15.6°C
61°F — 16.1°C
62°F — 16.7°C
63°F — 17.2°C
64°F — 17.8°C
San Diego
UNITED STATES
MEXICO
64°
63°
62°
60°
61°
64°
60
63°
61°
62°
62°
63°


33°00′
117°30′
117°00′
32°30′
31 MAY 1972
1402–1457 PDT
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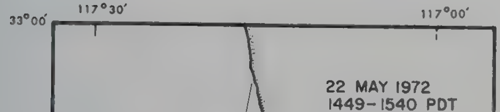
66°F — 18.9°C
67°F — 19.4°C
68°F — 20.0°C
San Diego
UNITED STATES
MEXICO
67°
67°
≥68°
66°
65°
65°
66°
<65°
67°
68°
68°
67°
66°
65°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117°00′
32°30′
22 MAY 1972
1449–1540 PDT
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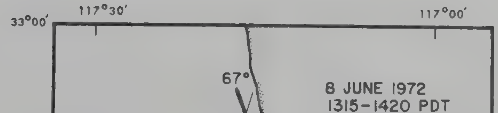
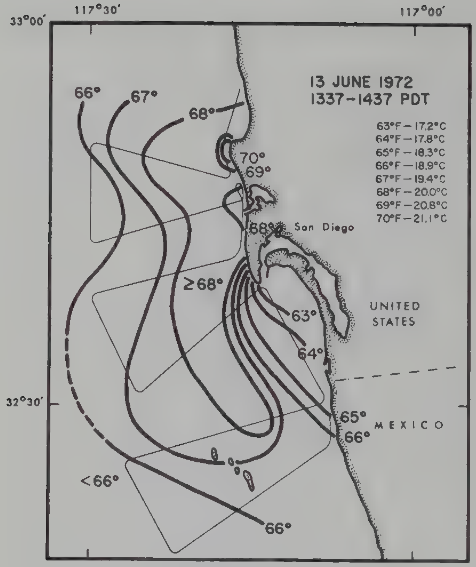
60°F — 15.6°C
61°F — 16.1°C
62°F — 16.7°C
63°F — 17.2°C
64°F — 17.8°C
San Diego
UNITED STATES
MEXICO
64°
≥
64°
59°
60°
61°
62°
63°


33°00′
117°30′
117°00′
32°30′
8 JUNE 1972
1315–1420 PDT
64°F — 17.8°C
65°F — 18.3°C
66°F — 18.9°C
67°F — 19.4°C
San Diego
UNITED STATES
MEXICO
67°
66°
≥67°
67°
<64°
64°
64°
65
66°
66°
65°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117°00′
32°30′
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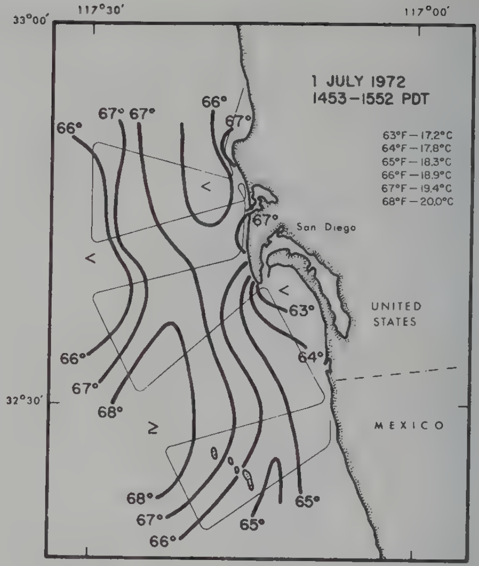
64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
69°F – 20.8°C
70°F – 21.1°C
66°
67°
68°
70°
69°
68°
San Diego
≥68°
63°
64°
65°
66°
UNITED STATES
MEXICO
<66°
66°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117°00′
32°30′
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1453-1552 PDT
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64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
66°
67°
67°
66°
67°
<
67°
San Diego
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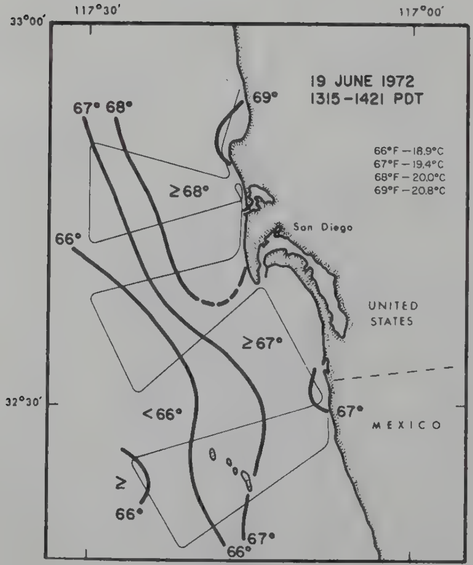
68°
67°
66°
65°
65°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117°30′
117°00′
32°30′
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1315-1421 PDT
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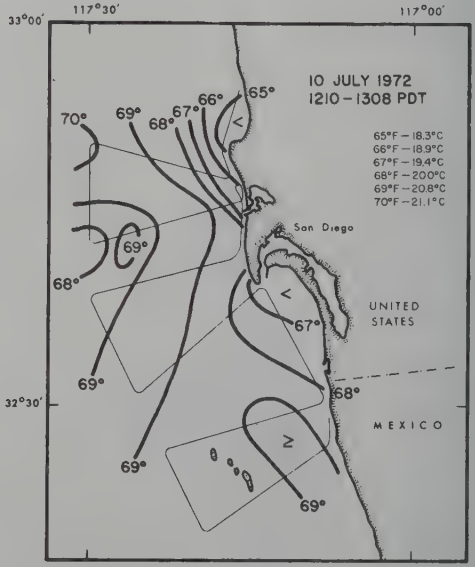
67°F – 19.4°C
68°F – 20.0°C
69°F – 20.8°C
67°
68°
69°
≥68°
San Diego
66°
UNITED STATES
≥67°
<66°
67°
MEXICO
≥
66°
66°
67°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117°30′
117°00′
32°30′
10 JULY 1972
1210-1308 PDT
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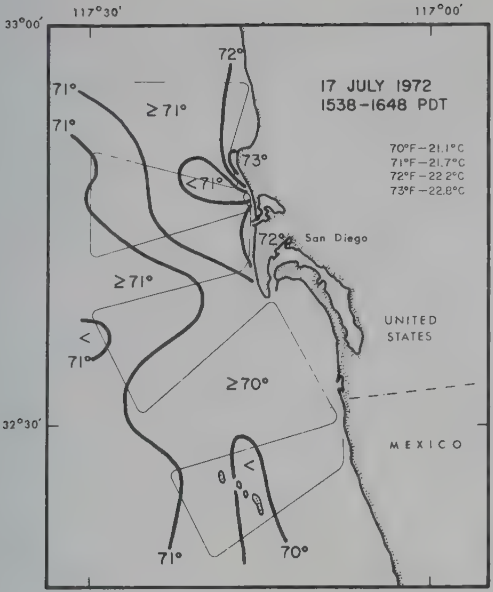
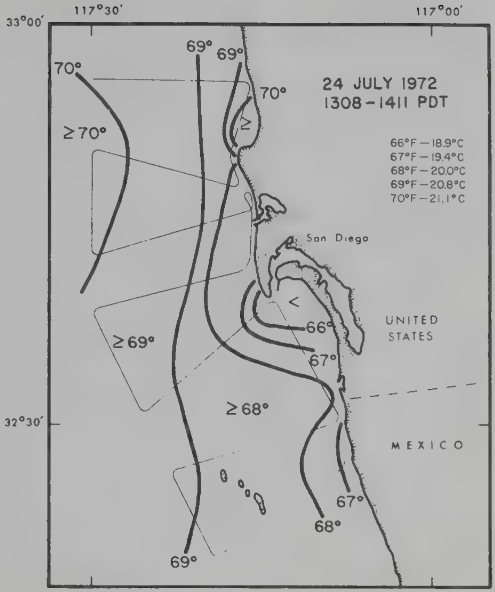
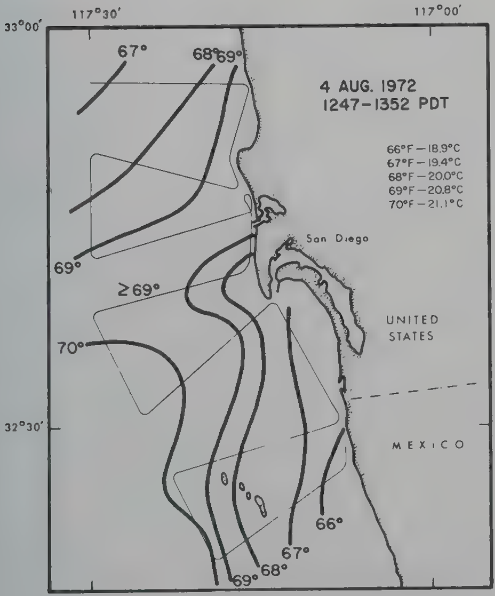
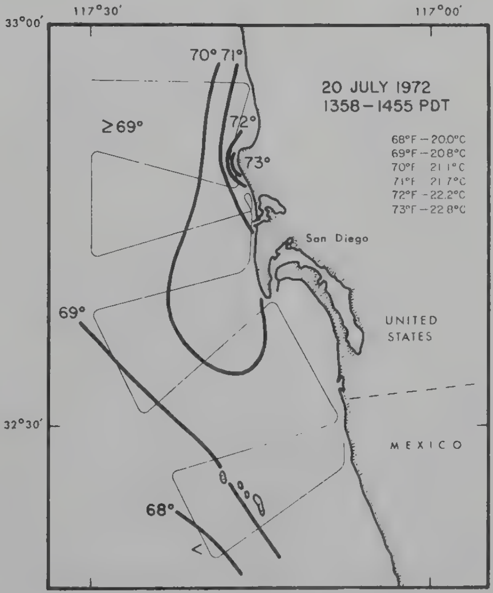
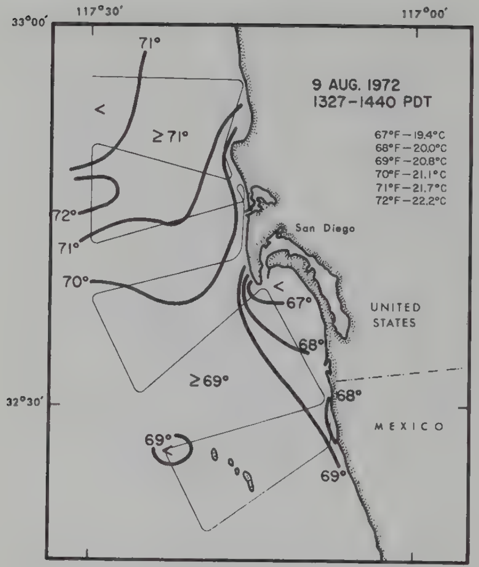
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
69°F – 20.8°C
70°F – 21.1°C
70°
69°
68°
67°
66°
65°
<
San Diego
69°
68°
<
67°
UNITED STATES
69°
68°
MEXICO
≥
69°
69°

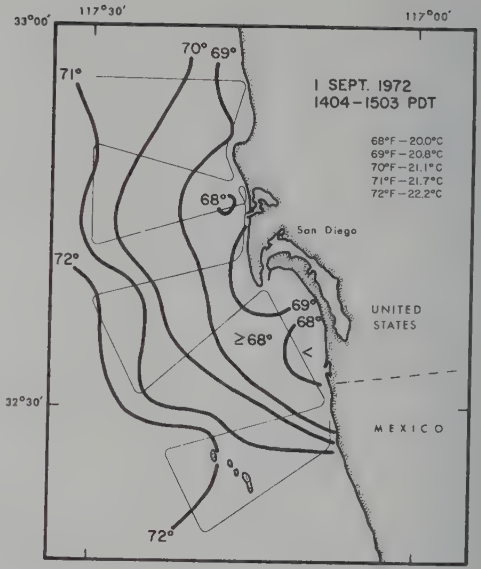

117°30′
117°00′
33°00′
32°30′
17 JULY 1972
1538-1648 PDT
70°F – 21.1°C
71°F – 21.7°C
72°F – 22.2°C
73°F – 22.8°C
72°
71°
71°
≥71°
73°
<71°
72°
San Diego
≥71°
<
71°
≥70°
UNITED STATES
MEXICO
<
71°
70°

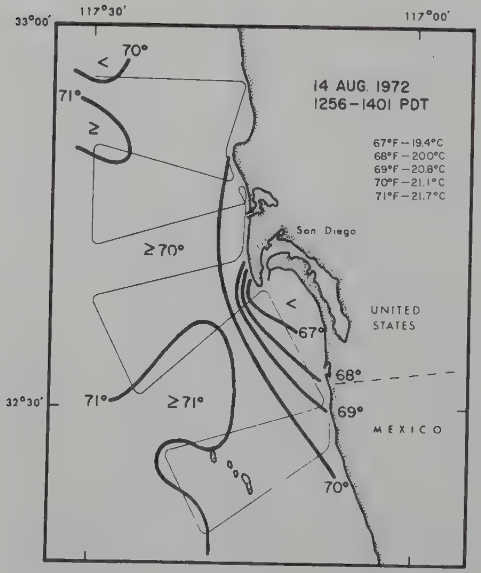

117°30′
117°00′
33°00′
32°30′
24 JULY 1972
1308-1411 PDT
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
69°F – 20.8°C
70°F – 21.1°C
69°
69°
70°
70°
≥70°
≥
San Diego
<
66°
67°
≥69°
≥68°
UNITED STATES
MEXICO
67°
68°
69°


117°30′
117°00′
33°00′
32°30′
4 AUG. 1972
1247-1352 PDT
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
69°F – 20.8°C
70°F – 21.1°C
67°
68°
69°
69°
≥69°
70°
San Diego
UNITED STATES
MEXICO
66°
67°
69°
68°


117°30′
117°00′
33°00′
32°30′
20 JULY 1972
1358 – 1455 PDT
68°F – 20.0°C
69°F – 20.8°C
70°F – 21.1°C
71°F – 21.7°C
72°F – 22.2°C
73°F – 22.8°C
70°
71°
≥69°
72°
73°
San Diego
69°
UNITED STATES
MEXICO
68°
<


33°00′
117°30′
117°00′
32°30′
9 AUG. 1972
1327–1440 PDT
67°F – 19.4°C
68°F – 20.0°C
69°F – 20.8°C
70°F – 21.1°C
71°F – 21.7°C
72°F – 22.2°C
71°
<
≥ 71°
72°
71°
70°
San Diego
<
67°
UNITED
STATES
68°
≥ 69°
68°
MEXICO
69°
69°


33°00′
117°30′
117°00′
32°30′
1 SEPT. 1972
1404–1503 PDT
68°F – 20.0°C
69°F – 20.8°C
70°F – 21.1°C
71°F – 21.7°C
72°F – 22.2°C
70°
69°
71°
68°
San Diego
72°
69°
68°
UNITED
STATES
≥ 68°
<
MEXICO
72°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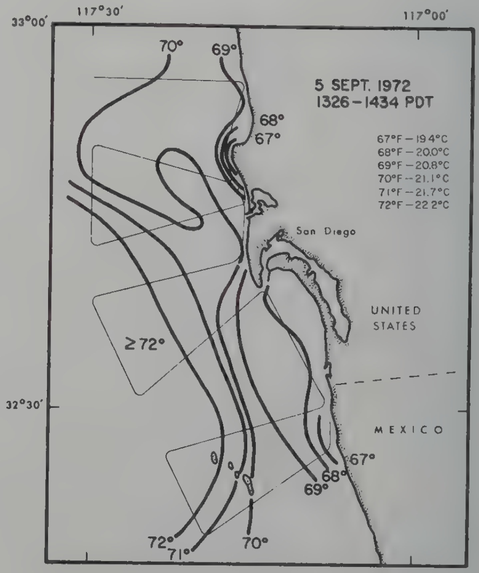
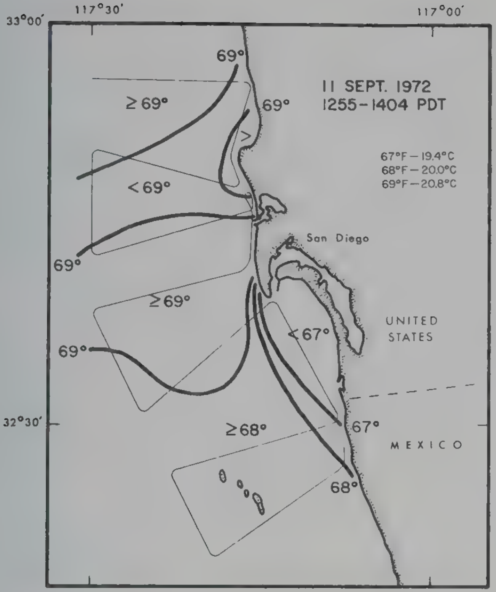
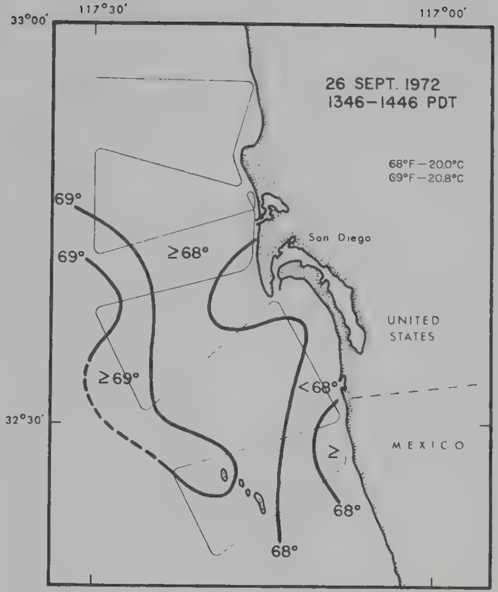
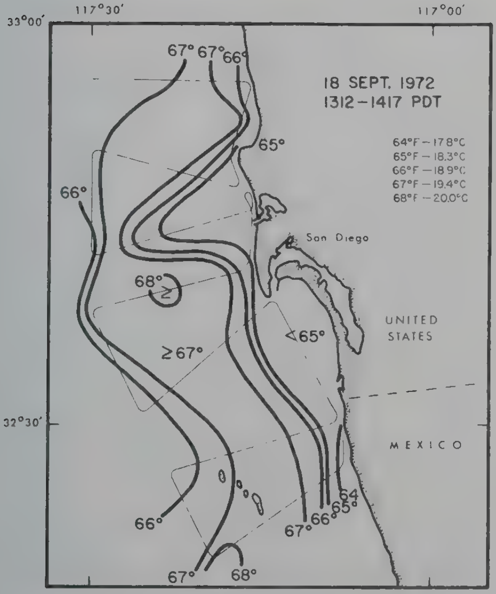
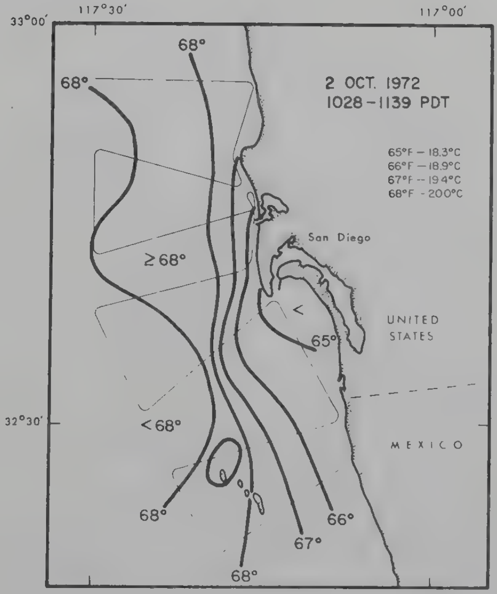
117°30′
117°00′
32°30′
14 AUG. 1972
1256–1401 PDT
67°F – 19.4°C
68°F – 20.0°C
69°F – 20.8°C
70°F – 21.1°C
71°F – 21.7°C
<
70°
71°
≥
≥ 70°
San Diego
<
67°
UNITED
STATES
68°
71°
≥ 71°
69°
MEXICO
70°

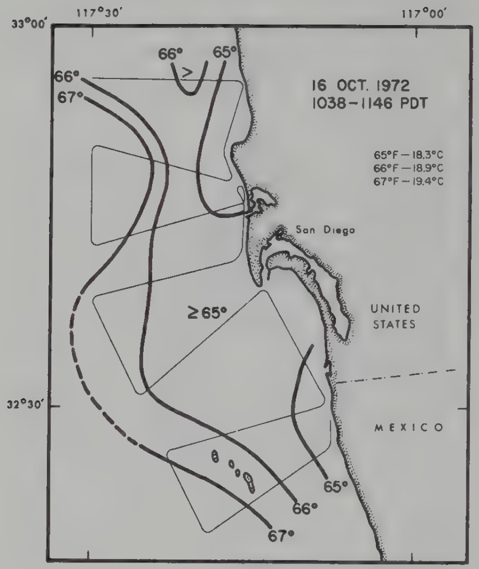

33°00′
117°30′
117°00′
32°30′
5 SEPT. 1972
1326–1434 PDT
67°F – 19.4°C
68°F – 20.0°C
69°F – 20.8°C
70°F – 21.1°C
71°F – 21.7°C
72°F – 22.2°C
70°
69°
68°
67°
San Diego
UNITED
STATES
≥ 72°
MEXICO
67°
68°
69°
72°
71°
70°


11 SEPT. 1972
1255–1404 PDT
67°F – 19.4°C
68°F – 20.0°C
69°F – 20.8°C
33°00′
117°30′
117°00′
32°30′
69°
≥ 69°
69°
>
< 69°
69°
San Diego
≥ 69°
< 67°
UNITED STATES
69°
≥ 68°
67°
MEXICO
68°


26 SEPT. 1972
1346–1446 PDT
68°F – 20.0°C
69°F – 20.8°C
33°00′
117°30′
117°00′
32°30′
69°
69°
≥ 68°
San Diego
UNITED STATES
≥ 69°
< 68°
≥
MEXICO
68°
68°

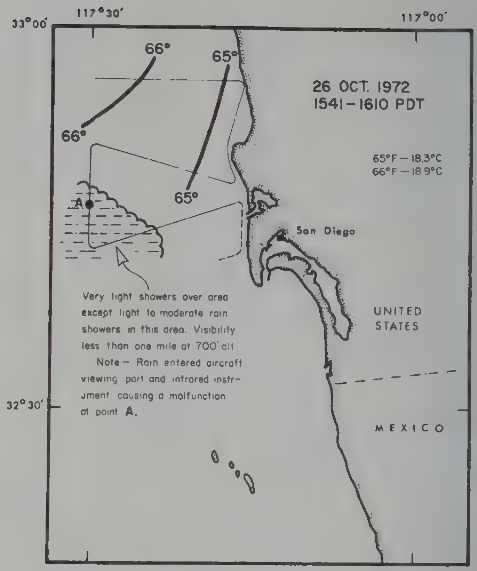

18 SEPT. 1972
1312–1417 PDT
64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
33°00′
117°30′
117°00′
32°30′
67°
67°
66°
65°
66°
San Diego
68°
≥
≥ 67°
< 65°
UNITED STATES
MEXICO
64
65°
66°
67°
66°
67°
68°


2 OCT. 1972
1028–1139 PDT
65°F – 18.3°C
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
33°00′
117°30′
117°00′
32°30′
68°
68°
San Diego
≥ 68°
<
65°
UNITED STATES
< 68°
MEXICO
68°
66°
67°
68°



16 OCT. 1972
1038–1146 PDT

33°00′
117°30′
117°00′
32°30′
66°
65°
66°
67°
≥65°
65°
66°
67°
San Diego
UNITED STATES
MEXICO
65°F — 18.3°C
66°F — 18.9°C
67°F — 19.4°C

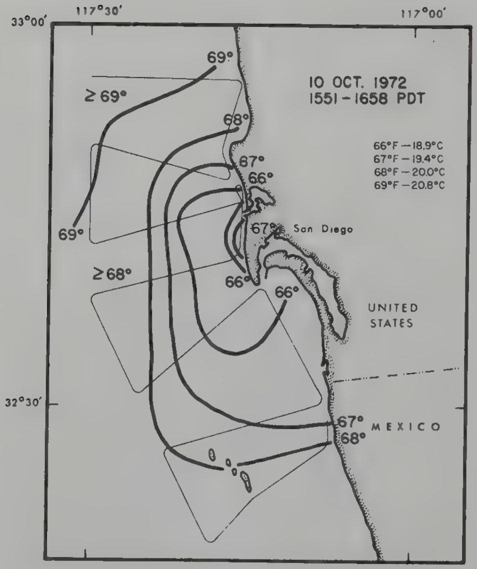


26 OCT. 1972
1541–1610 PDT

Very light showers over area except light to moderate rain showers in this area. Visibility less than one mile at 700′ alt

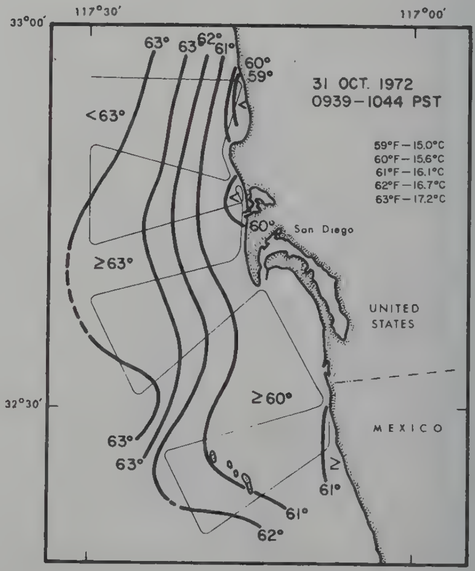
Note — Rain entered aircraft viewing port and infrared instrument causing a malfunction at point A.

33°00′
117°30′
117°00′
32°30′
66°
65°
66°
65°
A
San Diego
UNITED STATES
MEXICO
65°F — 18.3°C
66°F — 18.9°C



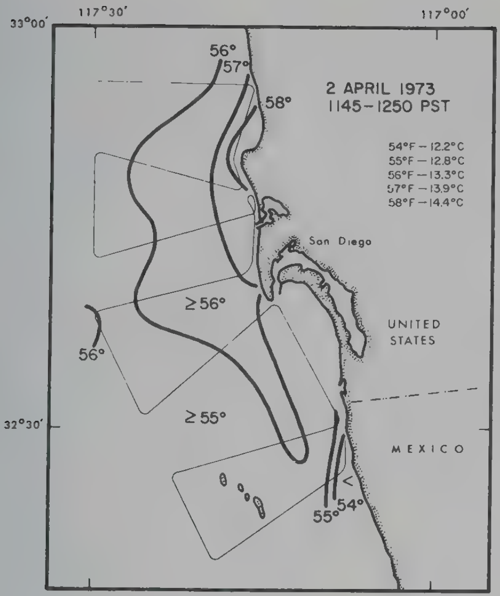
10 OCT. 1972
1551–1658 PDT

33°00′
117°30′
117°00′
32°30′
69°
≥69°
68°
67°
66°
69°
67°
≥68°
66°
66°
67°
68°
San Diego
UNITED STATES
MEXICO
66°F — 18.9°C
67°F — 19.4°C
68°F — 20.0°C
69°F — 20.8°C

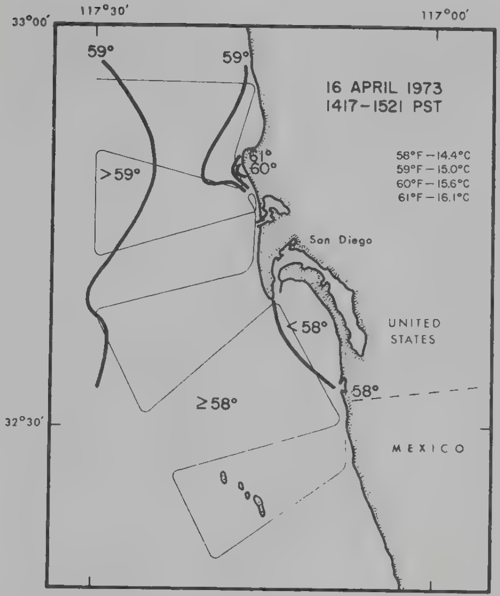


31 OCT. 1972
0939–1044 PST

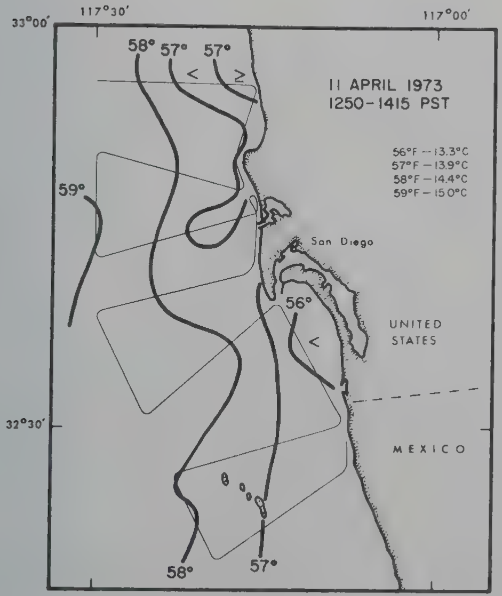
33°00′
117°30′
117°00′
32°30′
63°
63°
62°
61°
60°
59°
<63°
<
<
60°
≥63°
≥60°
63°
63°
≥
61°
61°
62°
San Diego
UNITED STATES
MEXICO
59°F — 15.0°C
60°F — 15.6°C
61°F — 16.1°C
62°F — 16.7°C
63°F — 17.2°C


2 APRIL 1973
1145–1250 PST

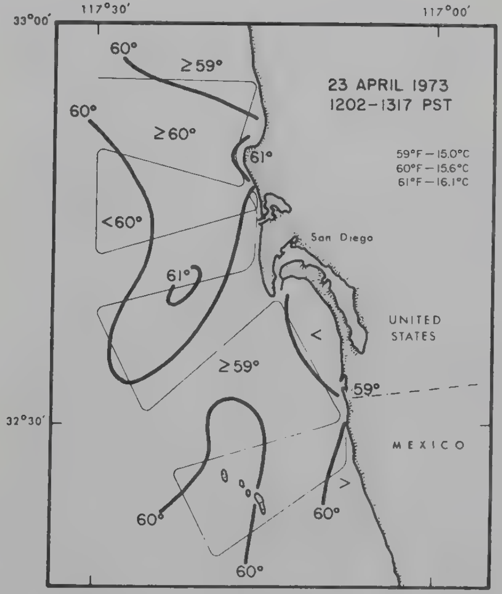
33°00′
117°30′
117°00′
32°30′
56°
57°
58°
54°F – 12.2°C
55°F – 12.8°C
56°F – 13.3°C
57°F – 13.9°C
58°F – 14.4°C
San Diego
≥56°
56°
UNITED STATES
≥55°
MEXICO
<
54°
55°


16 APRIL 1973
1417–1521 PST

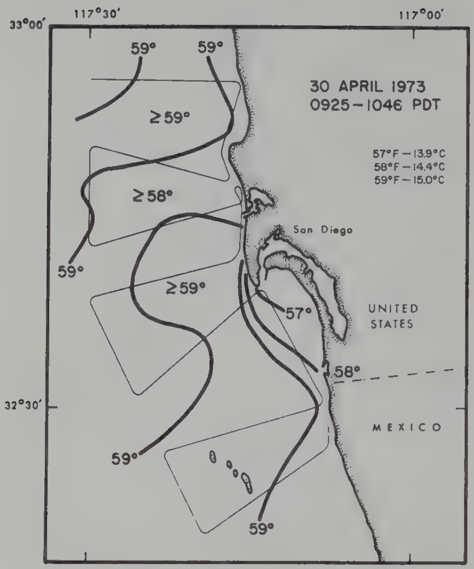
33°00′
117°30′
117°00′
32°30′
59°
59°
61°
60°
>59°
58°F – 14.4°C
59°F – 15.0°C
60°F – 15.6°C
61°F – 16.1°C
San Diego
<58°
UNITED STATES
58°
≥58°
MEXICO

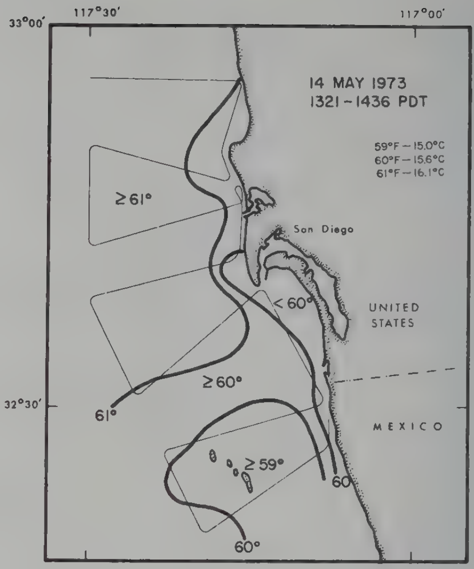

11 APRIL 1973
1250–1415 PST

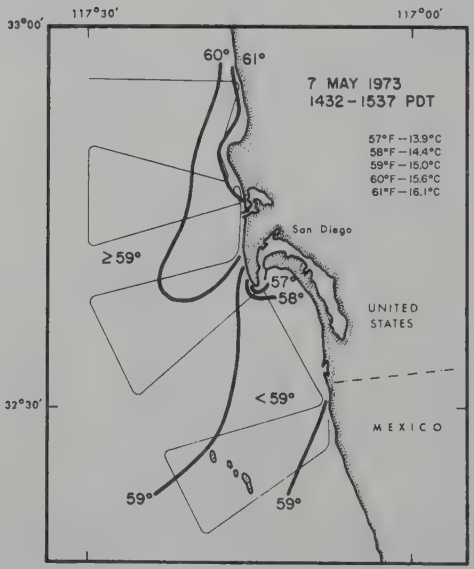
33°00′
117°30′
117°00′
32°30′
58°
57°
57°
<
>
56°F – 13.3°C
57°F – 13.9°C
58°F – 14.4°C
59°F – 15.0°C
59°
San Diego
56°
<
UNITED STATES
MEXICO
58°
57°

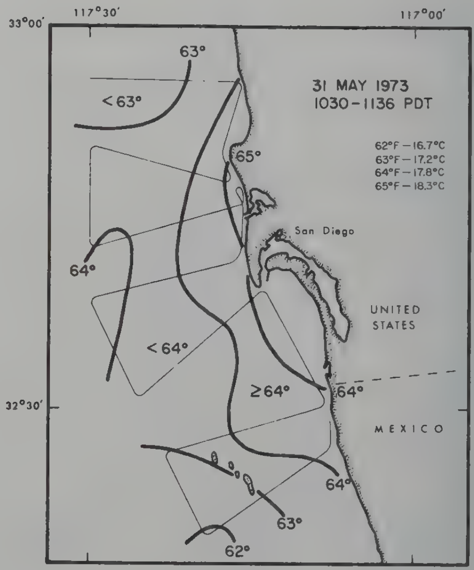

23 APRIL 1973
1202–1317 PST

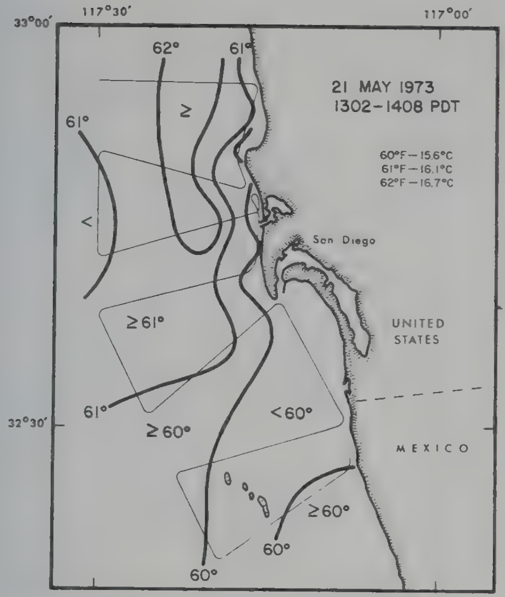
33°00′
117°30′
117°00′
32°30′
60°
≥59°
60°
≥60°
61°
59°F – 15.0°C
60°F – 15.6°C
61°F – 16.1°C
<60°
San Diego
61°
<
UNITED STATES
≥59°
59°
MEXICO
>
60°
60°
60°

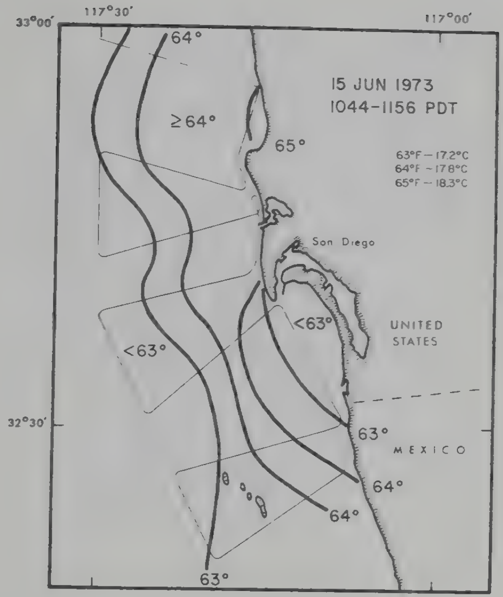

33°00'
117°30'
117°00'
30 APRIL 1973
0925–1046 PDT
57°F – 13.9°C
58°F – 14.4°C
59°F – 15.0°C
59°
59°
≥59°
≥58°
59°
San Diego
≥59°
57°
UNITED STATES
58°
32°30'
MEXICO
59°
59°

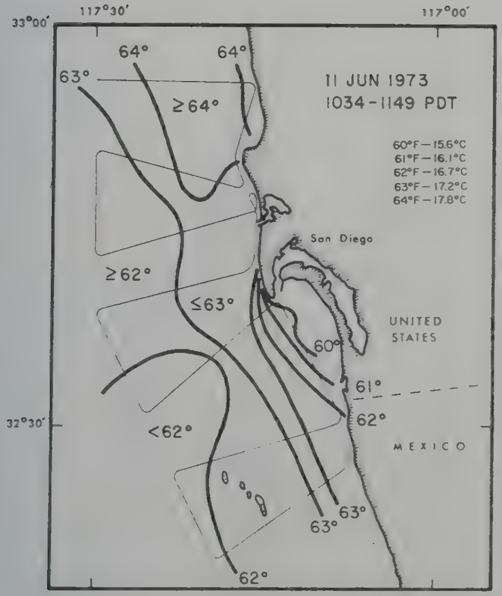

33°00'
117°30'
117°00'
14 MAY 1973
1321–1436 PDT
59°F – 15.0°C
60°F – 15.6°C
61°F – 16.1°C
≥61°
San Diego
<60°
UNITED STATES
≥60°
32°30'
61°
MEXICO
≥59°
60
60°

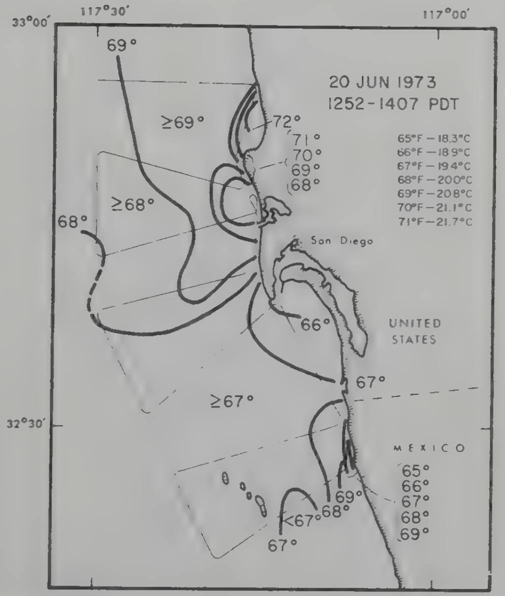

33°00'
117°30'
117°00'
60°
61°
7 MAY 1973
1432–1537 PDT
57°F – 13.9°C
58°F – 14.4°C
59°F – 15.0°C
60°F – 15.6°C
61°F – 16.1°C
San Diego
≥59°
57°
58°
UNITED STATES
<59°
32°30'
MEXICO
59°
59°

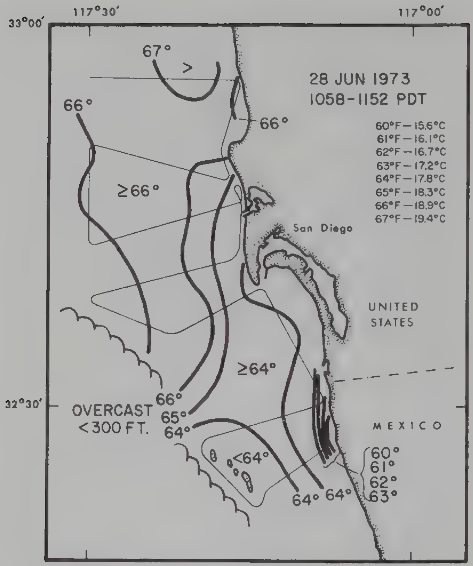

33°00'
117°30'
117°00'
63°
<63°
31 MAY 1973
1030–1136 PDT
62°F – 16.7°C
63°F – 17.2°C
64°F – 17.8°C
65°F – 18.3°C
65°
San Diego
64°
UNITED STATES
<64°
≥64°
64°
32°30'
MEXICO
64°
63°
62°

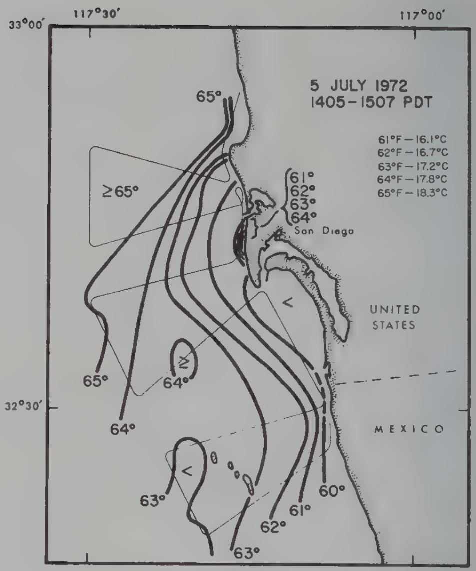

33°00′
117°30′
117°00′
32°30′
21 MAY 1973
1302-1408 PDT
60°F – 15.6°C
61°F – 16.1°C
62°F – 16.7°C
62°
61°
61°
≥
<
San Diego
≥61°
UNITED STATES
61°
≥60°
<60°
MEXICO
≥60°
60°
60°

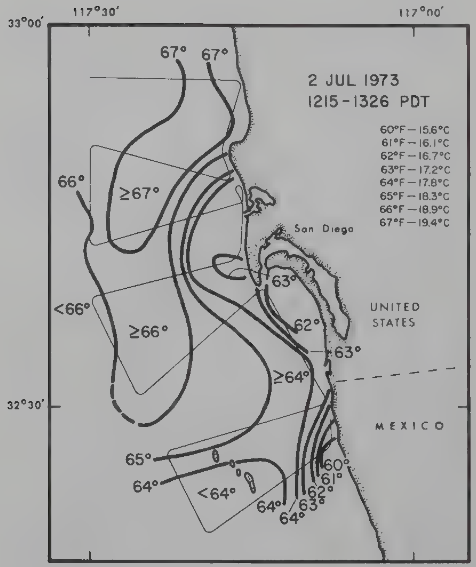

33°00′
117°30′
117°00′
32°30′
64°
15 JUN 1973
1044-1156 PDT
≥64°
65°
63°F – 17.2°C
64°F – 17.8°C
65°F – 18.3°C
San Diego
<63°
UNITED STATES
<63°
63°
MEXICO
64°
64°
63°

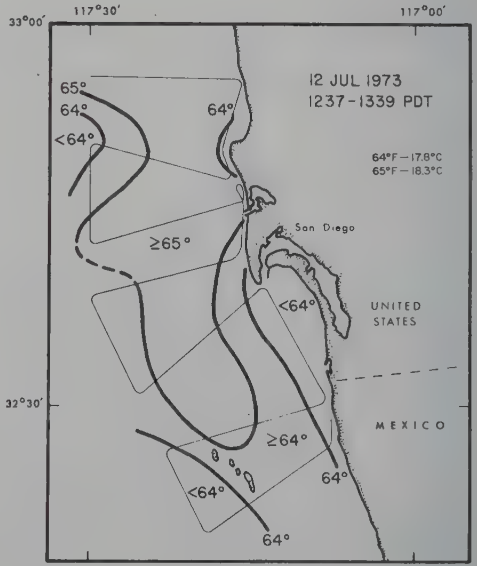

33°00′
117°30′
117°00′
32°30′
64°
64°
63°
11 JUN 1973
1034-1149 PDT
≥64°
60°F – 15.6°C
61°F – 16.1°C
62°F – 16.7°C
63°F – 17.2°C
64°F – 17.8°C
San Diego
≥62°
≤63°
UNITED STATES
60°
61°
62°
<62°
MEXICO
63°
63°
62°

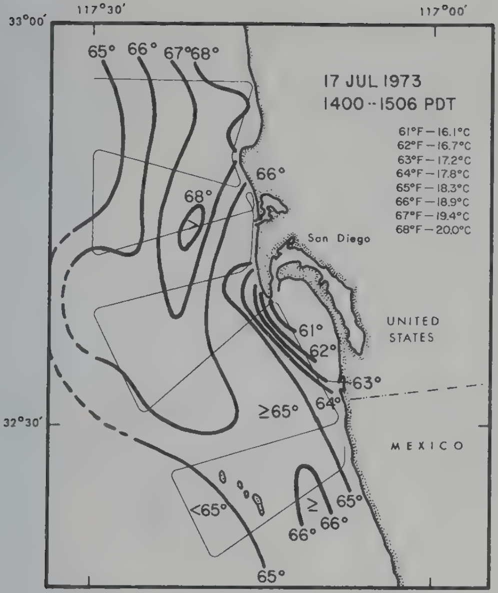

33°00′
117°30′
117°00′
32°30′
69°
20 JUN 1973
1252-1407 PDT
≥69°
72°
71°
70°
69°
68°
65°F – 18.3°C
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
69°F – 20.8°C
70°F – 21.1°C
71°F – 21.7°C
≥68°
68°
San Diego
66°
UNITED STATES
67°
≥67°
MEXICO
65°
66°
67°
68°
69°
69°
68°
<67°
67°

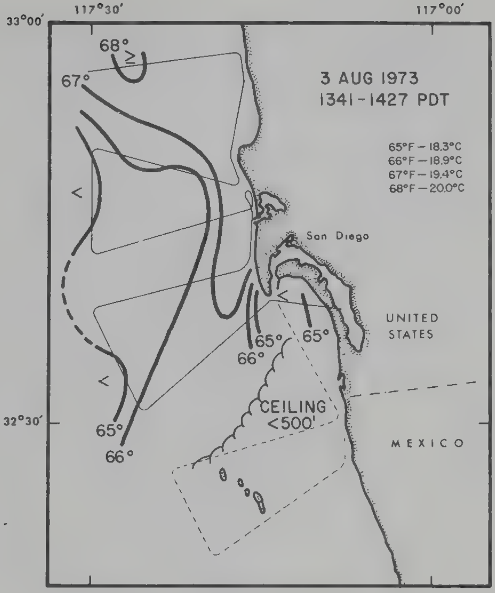

33°00'
117°30'
117°00'
32°30'
28 JUN 1973
1058-1152 PDT
60°F — 15.6°C
61°F — 16.1°C
62°F — 16.7°C
63°F — 17.2°C
64°F — 17.8°C
65°F — 18.3°C
66°F — 18.9°C
67°F — 19.4°C
67°
>
66°
66°
≥66°
San Diego
UNITED STATES
≥64°
66°
65°
64°
OVERCAST <300 FT.
MEXICO
<64°
60°
61°
62°
63°
64°
64°


33°00'
117°30'
117°00'
32°30'
5 JULY 1972
1405-1507 PDT
61°F — 16.1°C
62°F — 16.7°C
63°F — 17.2°C
64°F — 17.8°C
65°F — 18.3°C
65°
≥65°
61°
62°
63°
64°
San Diego
UNITED STATES
<
≥
65°
64°
64°
MEXICO
<
63°
60°
61°
62°
63°


33°00'
117°30'
117°00'
32°30'
2 JUL 1973
1215-1326 PDT
60°F — 15.6°C
61°F — 16.1°C
62°F — 16.7°C
63°F — 17.2°C
64°F — 17.8°C
65°F — 18.3°C
66°F — 18.9°C
67°F — 19.4°C
67°
67°
66°
≥67°
San Diego
63°
<66°
≥66°
62°
UNITED STATES
63°
≥64°
MEXICO
65°
60°
61°
64°
<64°
62°
63°
64°
64°


33°00'
117°30'
117°00'
32°30'
12 JUL 1973
1237-1339 PDT
64°F — 17.8°C
65°F — 18.3°C
65°
64°
<64°
64°
≥65°
San Diego
<64°
UNITED STATES
MEXICO
≥64°
64°
<64°
64°


33°00'
117°30'
117°00'
32°30'
17 JUL 1973
1400 - 1506 PDT
61°F – 16.1°C
62°F – 16.7°C
63°F – 17.2°C
64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
65° 66° 67° 68°
66°
68°
San Diego
61°
62°
63°
64°
≥65°
<65°
65°
66° 66°
65°
UNITED STATES
MEXICO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1341 - 1427 PDT
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67°F – 19.4°C
68°F – 20.0°C
68°
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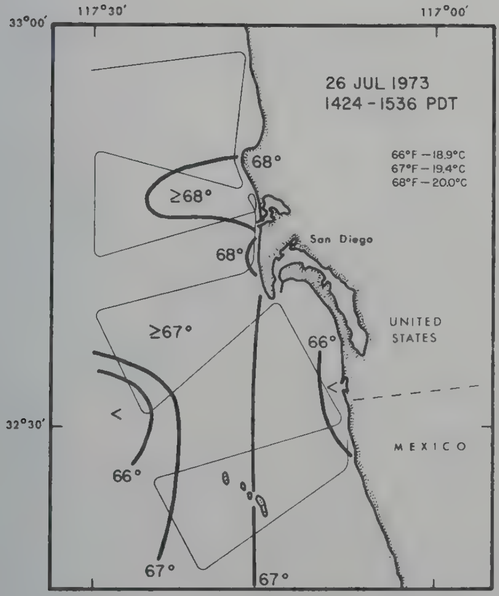
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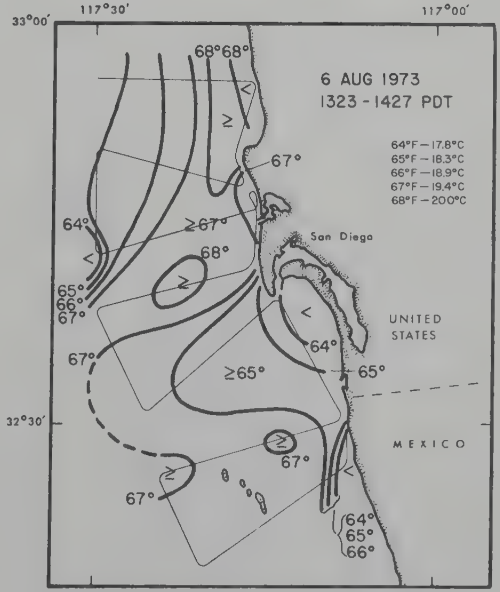
UNITED STATES
MEXICO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1323 - 1427 PDT
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65°F – 18.3°C
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
68° 68°
67°
≥67°
64°
68°
San Diego
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≥65°
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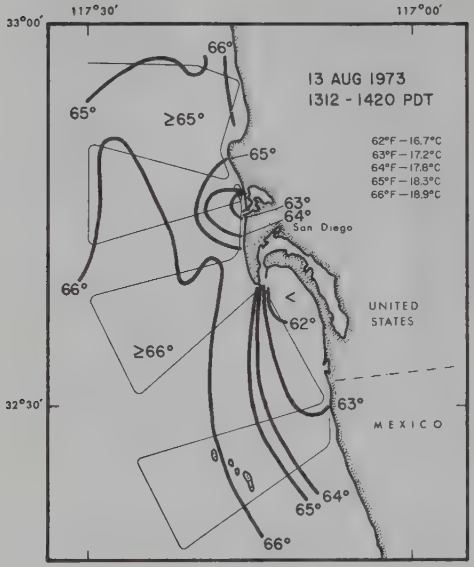
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1312 - 1420 PDT
62°F — 16.7°C
63°F — 17.2°C
64°F — 17.8°C
65°F — 18.3°C
66°F — 18.9°C
66°
65°
≥65°
65°
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San Diego
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<
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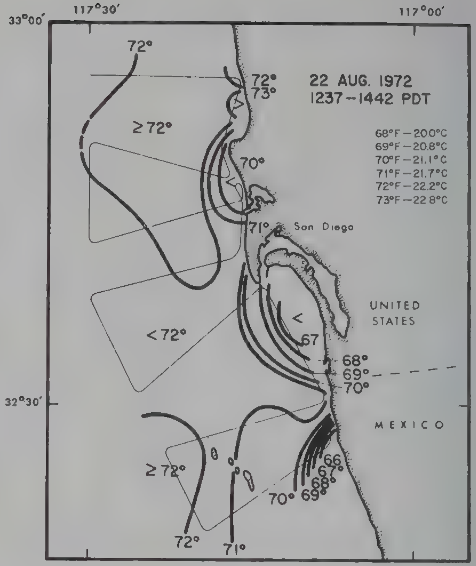
≥66°
63°
MEXICO
65°
64°
66°


117°30′
117°00′
33°00′
32°30′
22 AUG. 1972
1237 — 1442 PDT
68°F — 20.0°C
69°F — 20.8°C
70°F — 21.1°C
71°F — 21.7°C
72°F — 22.2°C
73°F — 22.8°C
72°
72°
73°
≥72°
70°
71°
San Diego
<72°
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MEXICO
≥72°
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67°
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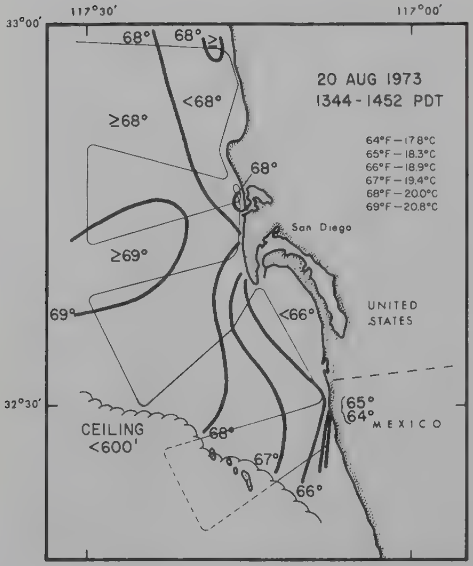
72°
71°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20 AUG 1973
1344 - 1452 PDT
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65°F — 18.3°C
66°F — 18.9°C
67°F — 19.4°C
68°F — 20.0°C
69°F — 20.8°C
68°
68°
≥
<68°
≥68°
68°
San Diego
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69°
<66°
UNITED STATES
CEILING <600′
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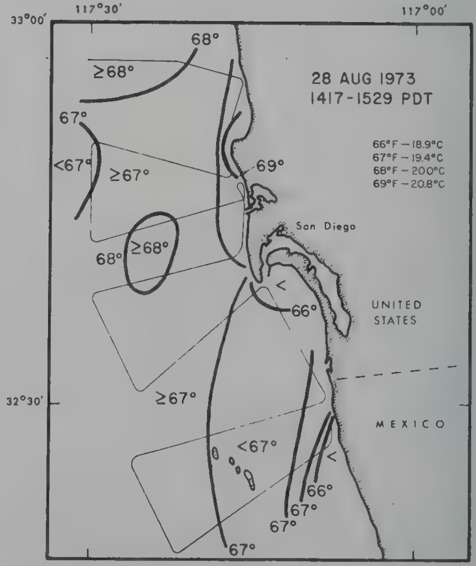
68°
67°
66°


117°30′
117°00′
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32°30′
28 AUG 1973
1417 - 1529 PDT
66°F — 18.9°C
67°F — 19.4°C
68°F — 20.0°C
69°F — 20.8°C
68°
≥68°
67°
<67°
≥67°
69°
San Diego
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≥68°
<
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UNITED STATES
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<67°
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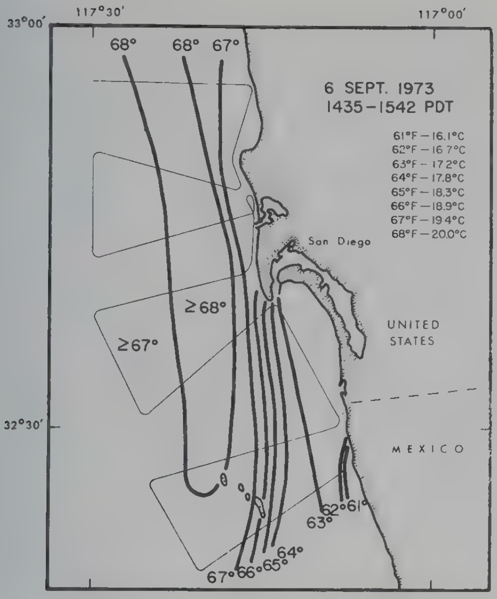
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1435–1542 PDT
61°F – 16.1°C
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63°F – 17.2°C
64°F – 17.8°C
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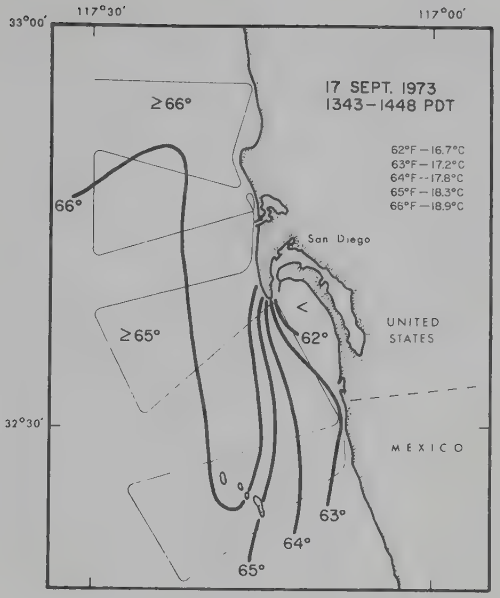
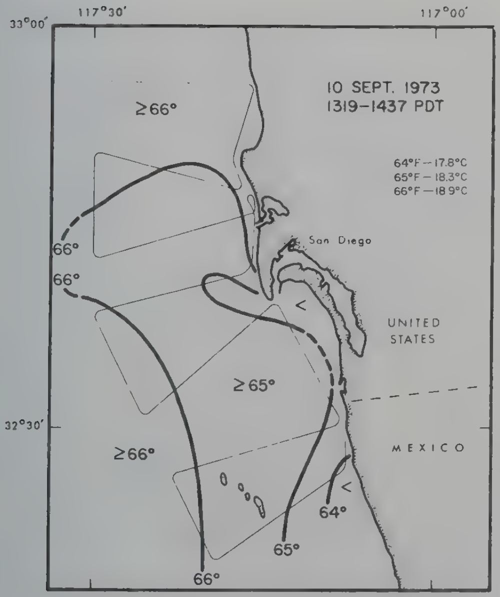
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
117°30′
117°00′
33°00′
32°30′
68°
68°
67°
≥68°
≥67°
San Diego
UNITED STATES
MEXICO
63°
62°
61°
64°
67°
66°
65°


17 SEPT. 1973
1343–1448 PDT
62°F – 16.7°C
63°F – 17.2°C
64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
117°30′
117°00′
33°00′
32°30′
≥66°
66°
San Diego
≥65°
<
62°
UNITED STATES
MEXICO
63°
64°
65°


10 SEPT. 1973
1319–1437 PDT
64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
117°30′
117°00′
33°00′
32°30′
≥66°
66°
66°
San Diego
<
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≥66°
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64°
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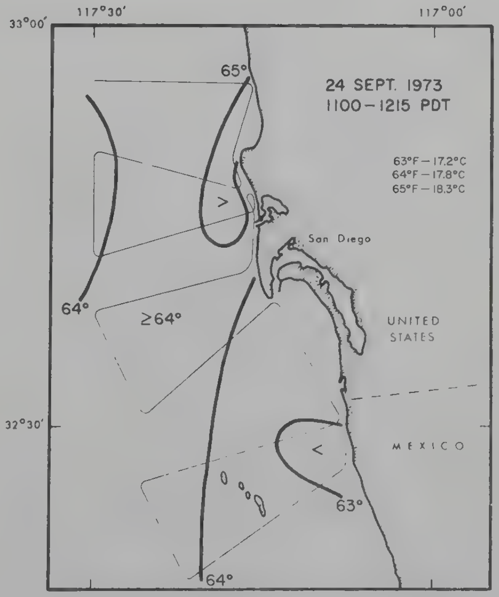
66°


24 SEPT. 1973
1100–1215 PDT
63°F – 17.2°C
64°F – 17.8°C
65°F – 18.3°C
117°30′
117°00′
33°00′
32°30′
65°
>
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≥64°
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<
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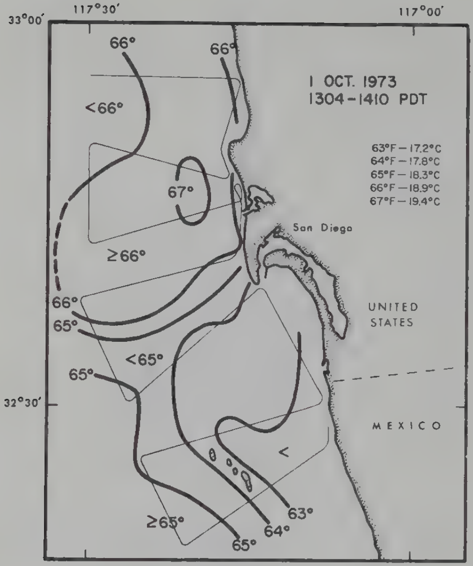
64°


33°00′
117°30′
117°00′
32°30′
1 OCT. 1973
1304-1410 PDT
63°F — 17.2°C
64°F — 17.8°C
65°F — 18.3°C
66°F — 18.9°C
67°F — 19.4°C
66°
66°
<66°
67°
≥66°
66°
65°
<65°
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≥65°
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64°
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<
San Diego
UNITED STATES
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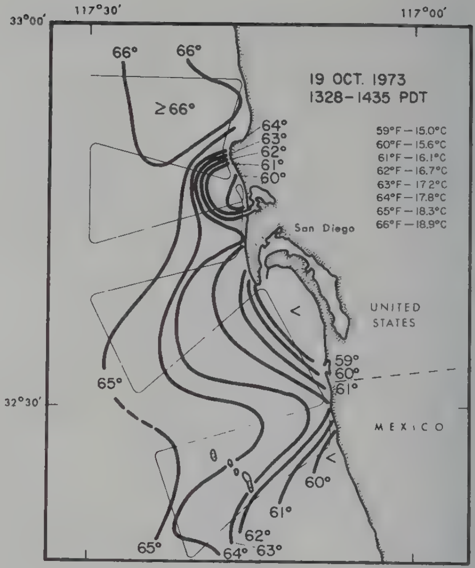
33°00′
117°30′
117°00′
32°30′
19 OCT. 1973
1328-1435 PDT
59°F — 15.0°C
60°F — 15.6°C
61°F — 16.1°C
62°F — 16.7°C
63°F — 17.2°C
64°F — 17.8°C
65°F — 18.3°C
66°F — 18.9°C
66°
66°
≥66°
64°
63°
62°
61°
60°
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59°
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61°
60°
61°
62°
63°
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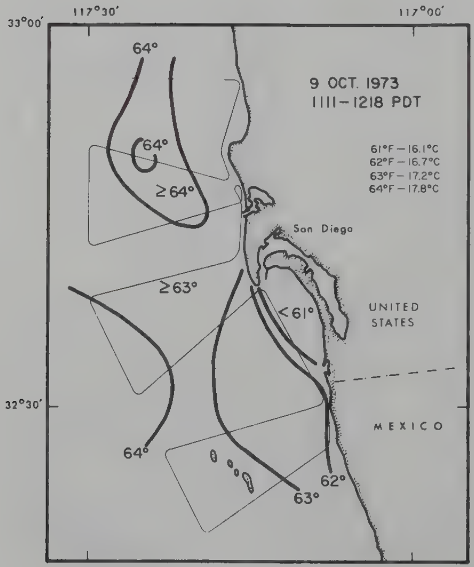
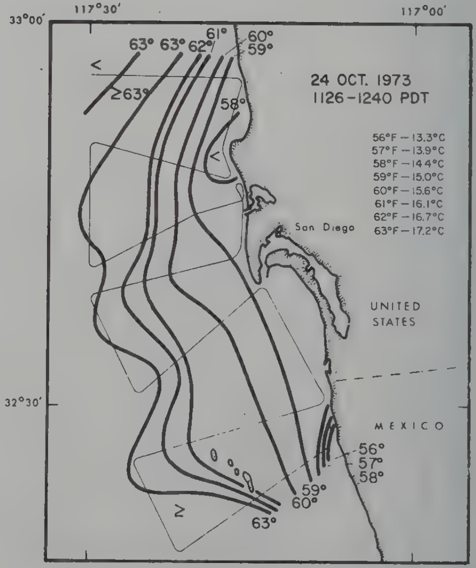
65°
<
<
San Diego
UNITED STATES
MEXICO


33°00′
117°30′
117°00′
32°30′
9 OCT. 1973
1111-1218 PDT
61°F — 16.1°C
62°F — 16.7°C
63°F — 17.2°C
64°F — 17.8°C
64°
64°
≥64°
≥63°
<61°
64°
63°
62°
San Diego
UNITED STATES
MEXICO


33°00′
117°30′
117°00′
32°30′
24 OCT. 1973
1126-1240 PDT
56°F — 13.3°C
57°F — 13.9°C
58°F — 14.4°C
59°F — 15.0°C
60°F — 15.6°C
61°F — 16.1°C
62°F — 16.7°C
63°F — 17.2°C
63°
63°
62°
61°
60°
59°
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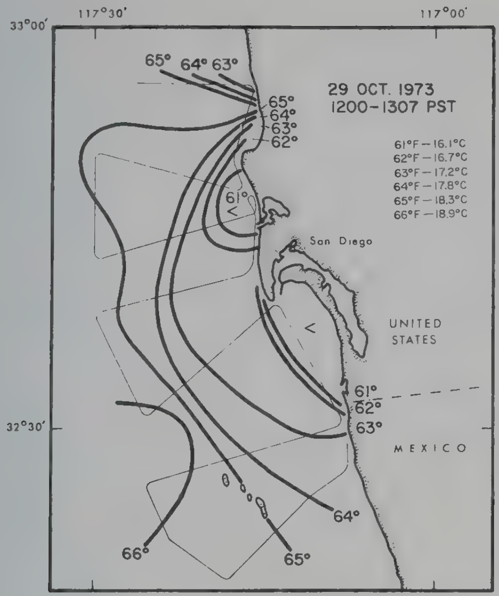
≥63°
58°
<
56°
57°
58°
59°
60°
63°
≥
San Diego
UNITED STATES
MEXICO


29 OCT. 1973
1200-1307 PST
61°F — 16.1°C
62°F — 16.7°C
63°F — 17.2°C
64°F — 17.8°C
65°F — 18.3°C
66°F — 18.9°C
117°30′
117°00′
33°00′
32°30′
65°
64°
63°
65°
64°
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61°
<
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<
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62°
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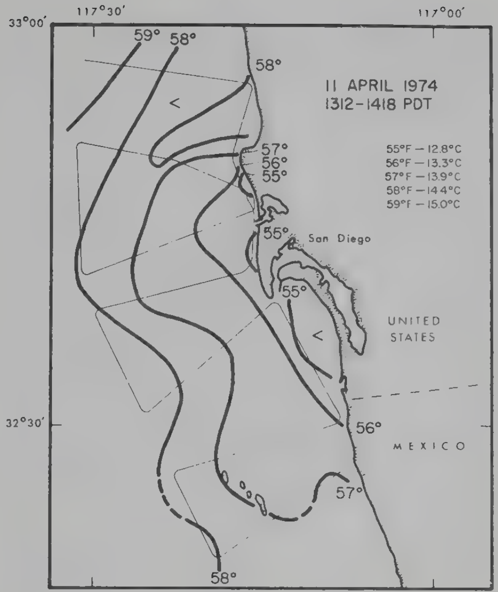
MEXICO
64°
66°
65°


11 APRIL 1974
1312-1418 PDT
55°F — 12.8°C
56°F — 13.3°C
57°F — 13.9°C
58°F — 14.4°C
59°F — 15.0°C
117°30′
117°00′
33°00′
32°30′
59°
58°
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56°
55°
55°
San Diego
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<
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56°
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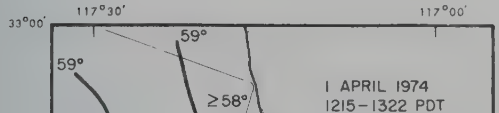
57°
58°


1 APRIL 1974
1215-1322 PDT
57°F — 13.9°C
58°F — 14.4°C
59°F — 15.0°C
60°F — 15.6°C
117°30′
117°00′
33°00′
32°30′
59°
59°
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San Diego
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≥59°
UNITED STATES
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MEXICO
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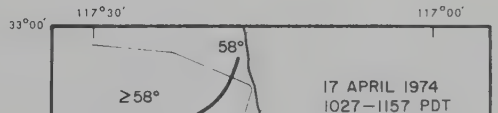
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1027-1157 PDT
55°F — 12.8°C
56°F — 13.3°C
57°F — 13.9°C
58°F — 14.4°C
117°30′
117°00′
33°00′
32°30′
58°
≥58°
<58°
San Diego
58°
UNITED STATES
<58°
MEXICO
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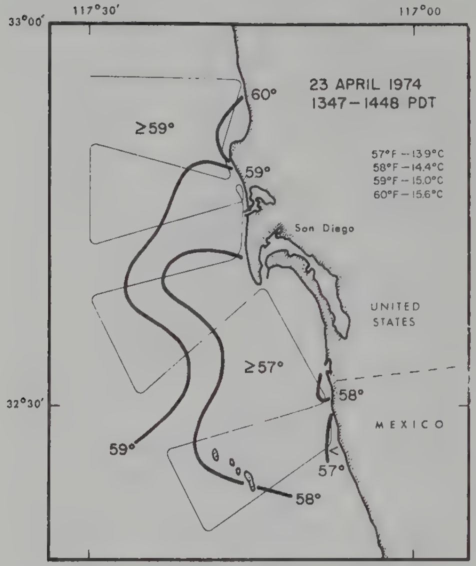
23 APRIL 1974
1347–1448 PDT
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58°F – 14.4°C
59°F – 15.0°C
60°F – 15.6°C
33°00′
117°30′
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≥59°
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≥57°
58°
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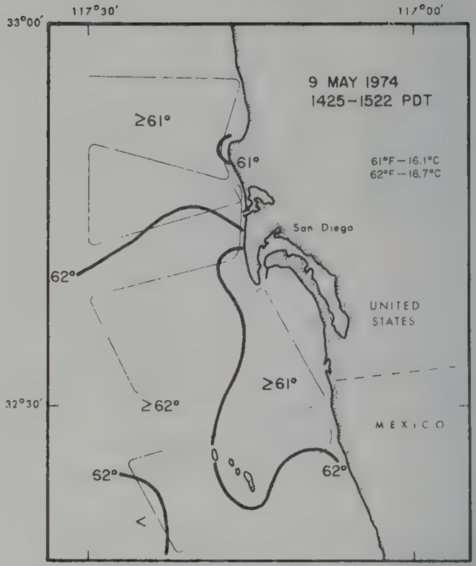
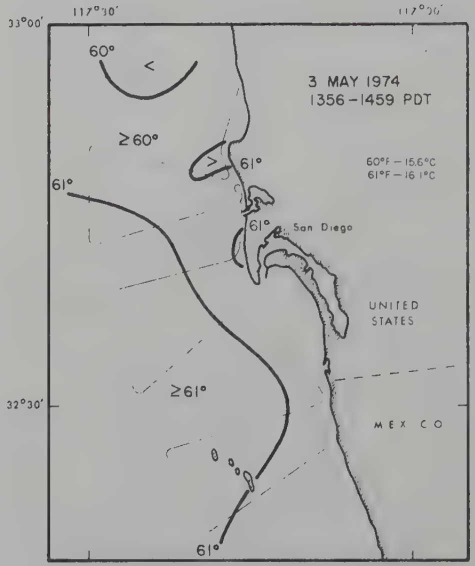
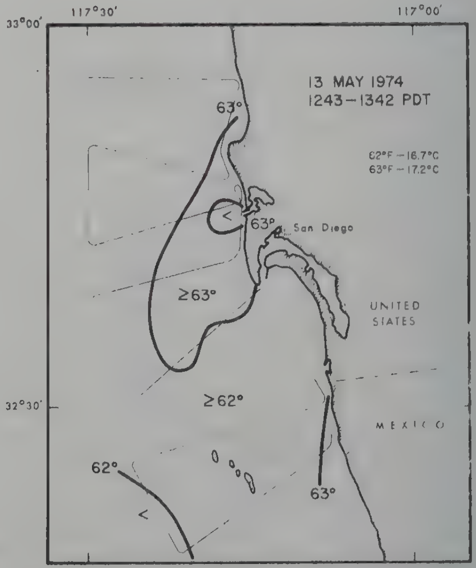
58°
San Diego
UNITED STATES
MEXICO


9 MAY 1974
1425–1522 PDT
61°F – 16.1°C
62°F – 16.7°C
33°00′
117°30′
117°00′
32°30′
≥61°
61°
62°
≥62°
≥61°
62°
62°
San Diego
UNITED STATES
MEXICO


3 MAY 1974
1356–1459 PDT
60°F – 15.6°C
61°F – 16.1°C
33°00′
117°30′
117°00′
32°30′
60°
≥60°
61°
61°
61°
≥61°
61°
San Diego
UNITED STATES
MEXICO


13 MAY 1974
1243–1342 PDT
62°F – 16.7°C
63°F – 17.2°C
33°00′
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63°
≥63°
≥62°
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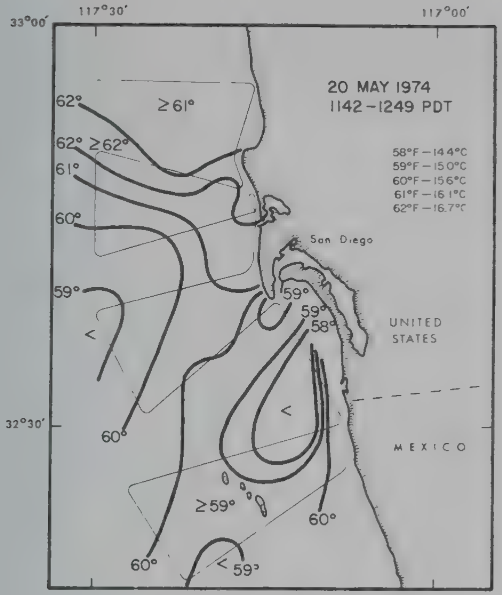
63°
San Diego
UNITED STATES
MEXICO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32°30′
20 MAY 1974
1142–1249 PDT
58°F – 14.4°C
59°F – 15.0°C
60°F – 15.6°C
61°F – 16.1°C
62°F – 16.7°C
≥61°
62°
62° ≥62°
61°
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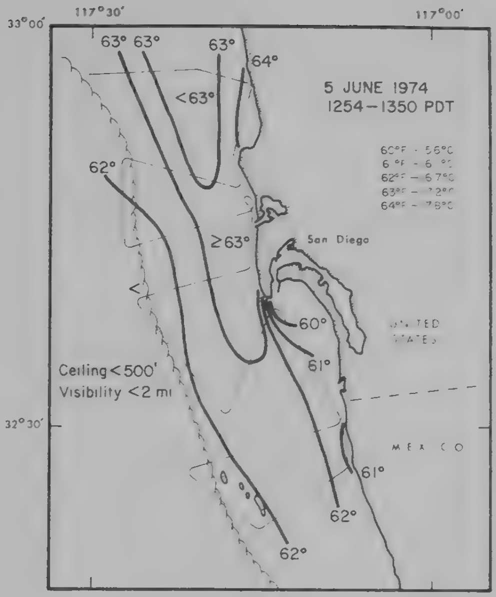
≥59°
60°
60°
< 59°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117°00′
33°00′
32°30′
63° 63°
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64°
<63°
5 JUNE 1974
1254–1350 PDT
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61°F – 16.1°C
62°F – 16.7°C
63°F – 17.2°C
64°F – 17.8°C
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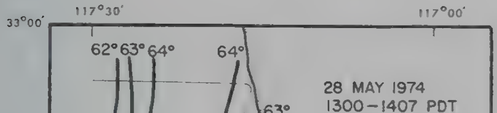
61°
62°
62°


117°30′
117°00′
33°00′
32°30′
62° 63° 64°
64°
63°
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28 MAY 1974
1300–1407 PDT
62°F – 16.7°C
63°F – 17.2°C
64°F – 17.8°C
San Diego
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62°
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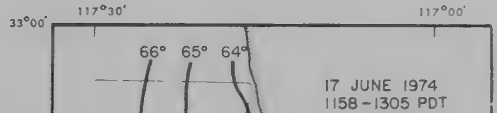
MEXICO
63° 62°
63°
62°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117°00′
33°00′
32°30′
66° 65° 64°
17 JUNE 1974
1158–1305 PDT
55°F – 12.8°C
56°F – 13.3°C
57°F – 13.9°C
58°F – 14.4°C
59°F – 15.0°C
60°F – 15.6°C
61°F – 16.1°C
62°F – 16.7°C
63°F – 17.2°C
64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
≥66°
San Diego
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57°
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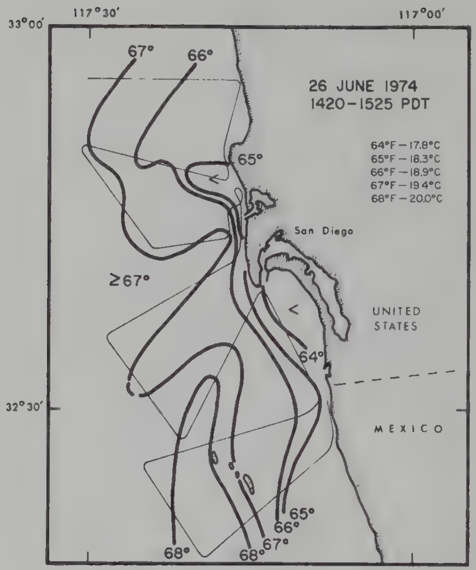
60° 59°
61°
62°
63°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26 JUNE 1974
1420–1525 PDT
64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
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65°
≥67°
64°
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67°
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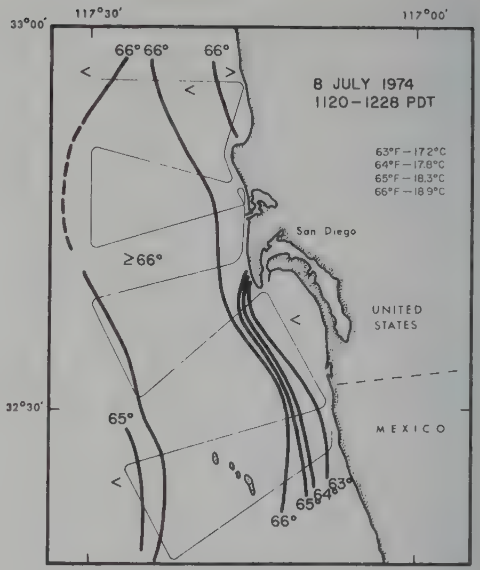
68°
San Diego
UNITED STATES
MEXICO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117°00′
33°00′
32°30′
8 JULY 1974
1120–1228 PDT
63°F – 17.2°C
64°F – 17.8°C
65°F – 18.3°C
66°F – 18.9°C
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San Diego
UNITED STATES
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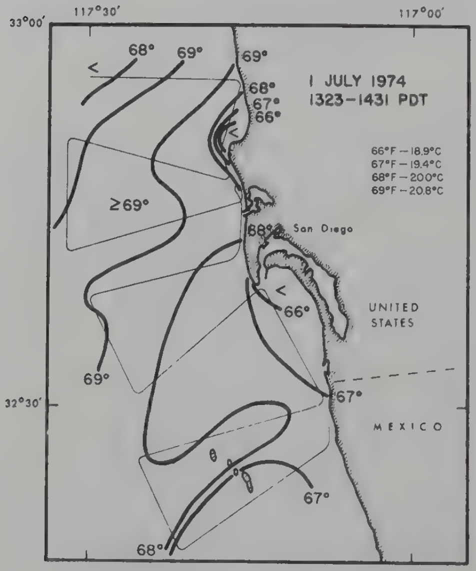
117°30′
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33°00′
32°30′
1 JULY 1974
1323–1431 PDT
66°F – 18.9°C
67°F – 19.4°C
68°F – 20.0°C
69°F – 20.8°C
68°
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≥69°
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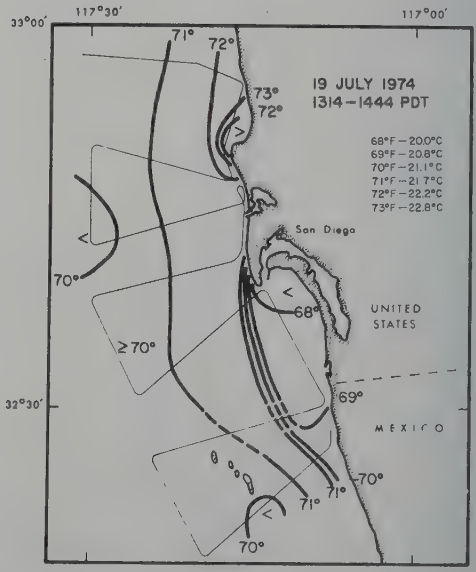
San Diego
UNITED STATES
MEXICO


117°30′
117°00′
33°00′
32°30′
19 JULY 1974
1314–1444 PDT
68°F – 20.0°C
69°F – 20.8°C
70°F – 21.1°C
71°F – 21.7°C
72°F – 22.2°C
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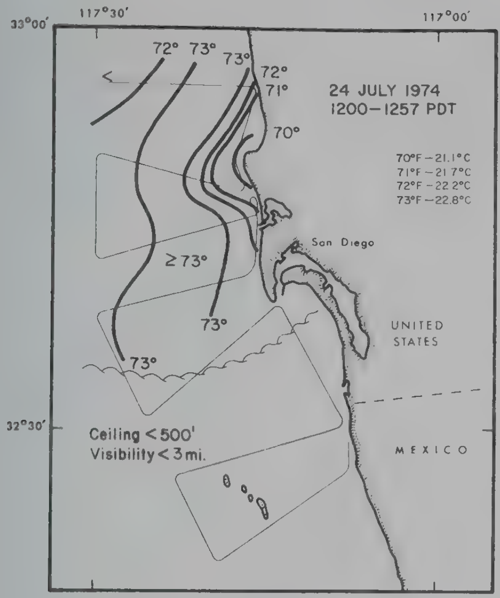
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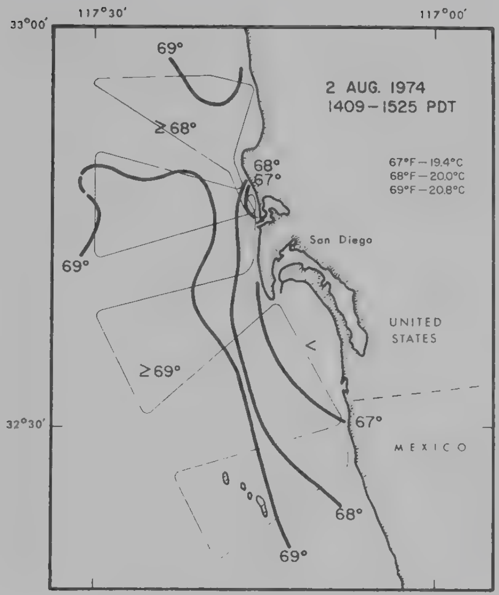
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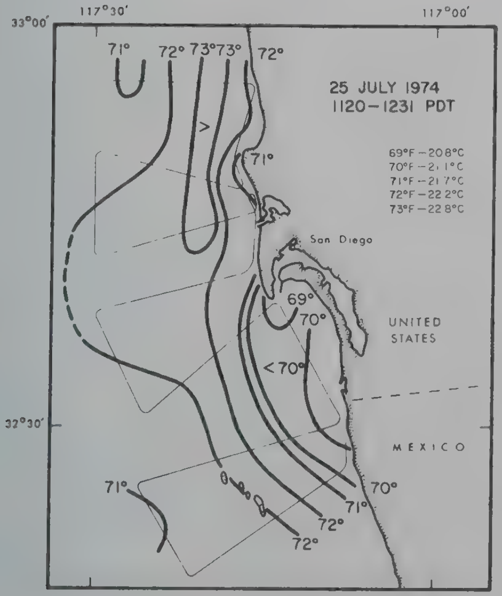
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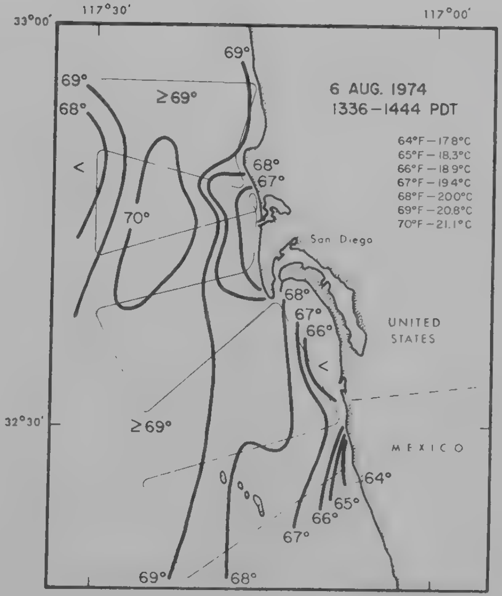
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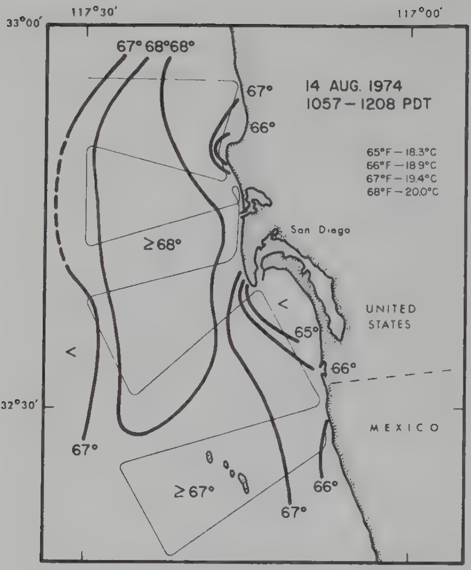
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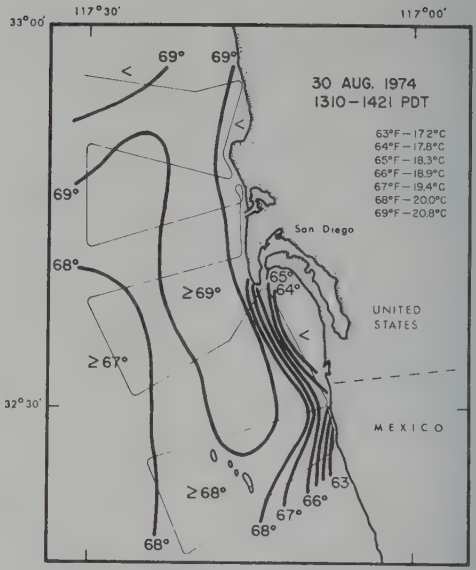
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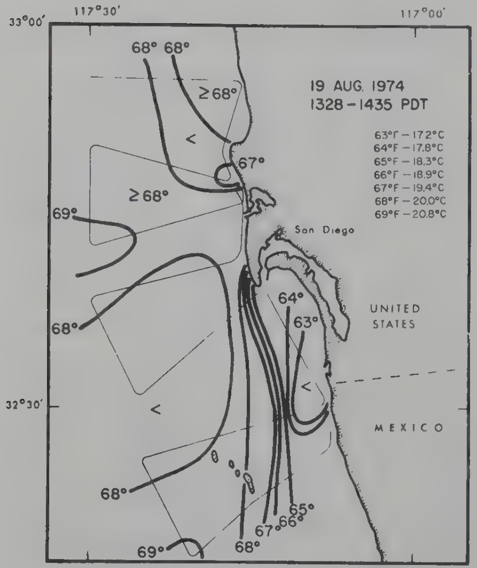
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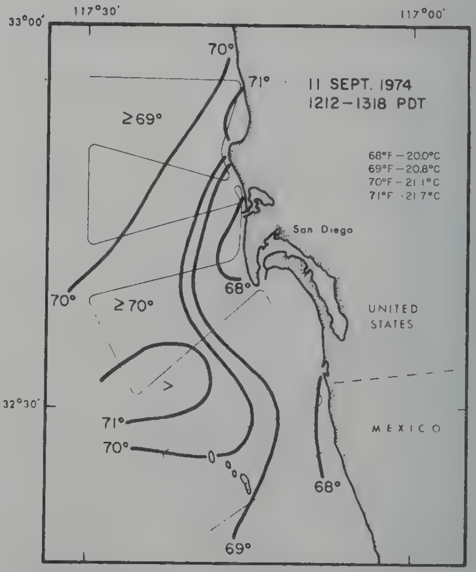
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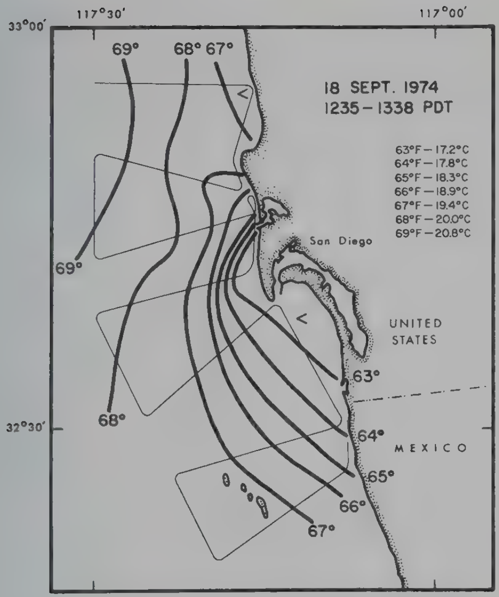
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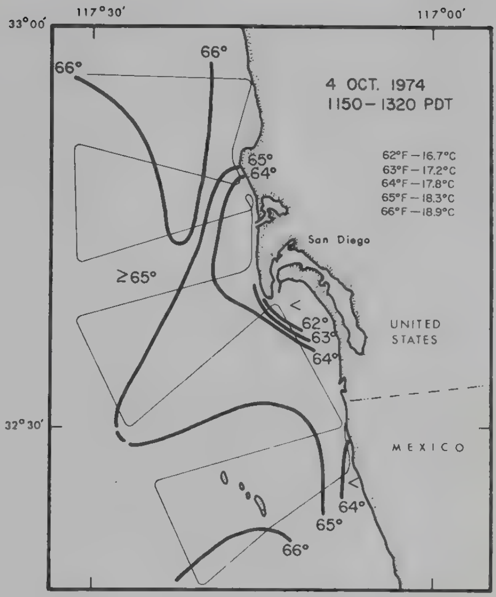
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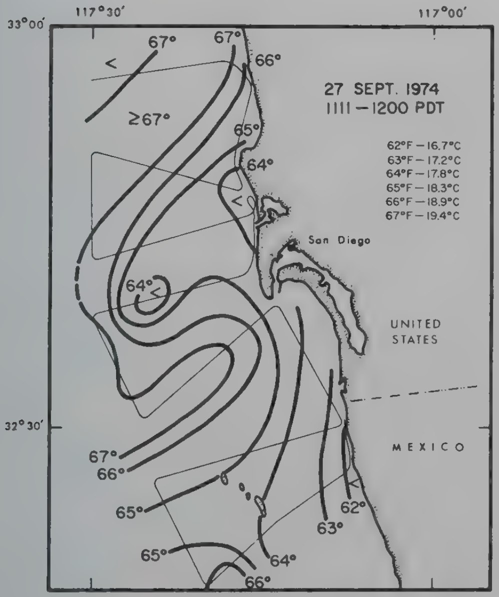
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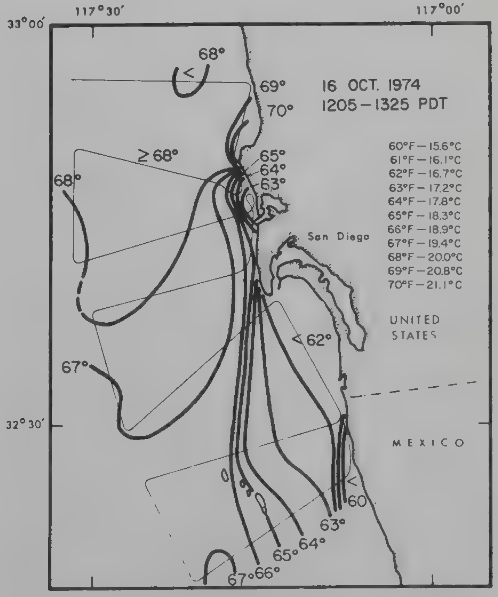
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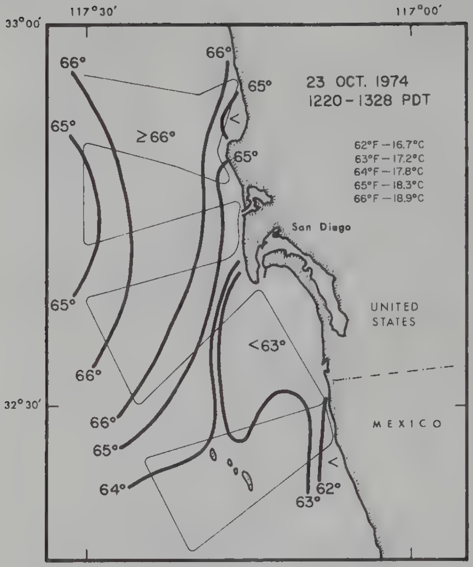
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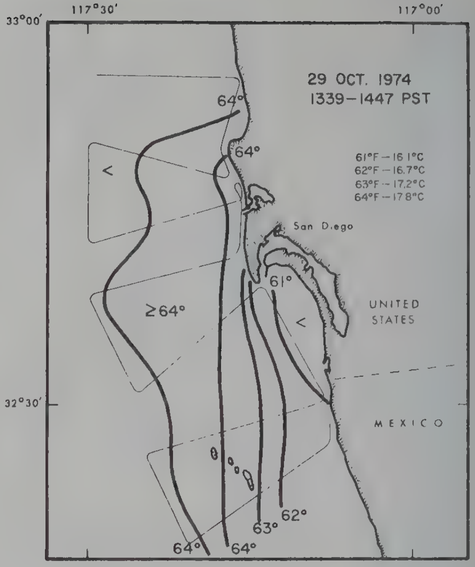
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783

EFFECT OF STARVATION ON THE HISTOLOGICAL AND MORPHOLOGICAL CHARACTERISTICS OF JACK MACKEREL, *TRACHURUS SYMMETRICUS*, LARVAE

Gail H. Theilacker[1]

ABSTRACT

Histological and morphological criteria were developed to assess the nutritional condition of laboratory-reared jack mackerel, *Trachurus symmetricus*, larvae. A comparison of the histological features of fed and starved larvae revealed that the digestive tract and its associated glands were the first tissues to be affected by starvation. The extent of cellular deterioration increased with time of starvation. To classify larval condition, histological characteristics of the pancreas and gut were given numerical grades. The histological technique correctly classified 83% of the feeding and starving larvae.

The morphometric analysis relied upon a stepwise discriminant analysis that used a combination of five measurements (standard length, head length, eye diameter, body depth at the pectoral, and body depth at the anus) to estimate individual larval condition. The morphometric method was as sensitive as the histological examination in determining whether or not a larva was fed or starved. Ultimately, these histological and morphological criteria may be useful for estimating larval survival in the field by assessing the condition of sea-caught larvae.

Fishery scientists generally agree that observed fluctuations in recruitment of young fish to a fish stock may be the consequence of mortality during the larval stage. Because starvation is probably one of the principal causes of mortality (Hunter 1976a), a need exists to develop criteria for detecting the incidence of starvation in sea-caught specimens. Several scientists have suggested that the differences in body form between feeding and starving larvae could be used to identify the nutritional status of larvae caught in sea surveys. For example, Shelbourne (1957) based his assessment of the condition of ocean-caught plaice, *Pleuronectes platessa,* larvae on their external appearance. Certain morphometric measurements also can be indicative of starvation. A decrease in thickness of the larval fish body has been correlated with starvation for several marine and freshwater fish larvae [herring, *Clupea harengus*, and plaice (Ehrlich et al. 1976); northern anchovy, *Engraulis mordax* (Arthur 1976); anchovy, *E. japonica* (Honjo et al. 1959; Nakai et al. 1969); pike, *Esox lucius*, and carp, *Cyprinus carpio* (Kostomarova 1962)]. Other morphological features (Ehrlich et al. 1976) considered to be indicative of starvation in herring and plaice were a decrease in the angle of the pectoral girdle, a change in the ratio of the head to eye height (herring only), and a decrease in the relative condition factor. Coincident with morphometric differences caused by starvation, Ehrlich et al. (1976) described histological changes in the gut and liver. The histological approach was used to classify yellowtail, *Seriola quinqueradiata*, larvae into "feeding," "semi-feeding," and "starving" groups by Umeda and Ochiai (1975). This technique was also effective for diagnosing starvation in northern anchovy larvae (O'Connell 1976). In both species, degeneration of cells of digestive organs was the best indicator for identification of starvation. Several other studies also have correlated starvation in fish larvae with degeneration of the digestive organs, mainly the gut. Kostomarova (1962) described a retardation in development of the gut in larvae of starved carp and pike and a reduction in the depth of the epithelial cells lining the gut. Reduced gut cell height was also reported for the larvae of starved yellowtail (Umeda and Ochiai 1975), herring, and plaice (Ehrlich et al. 1976).

Morphological criteria are preferable to histological ones because they take much less time to determine and require no special preservation techniques. However, histological criteria may be more accurate for classifying individual larva.

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

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The purpose of this study was to develop morphological and histological criteria for assessing the nutritional condition of jack mackerel larvae and to evaluate these criteria by comparing their success in identifying fed and starved larvae reared in the laboratory. Ultimately, criteria based on these results may be useful for estimating larval survival in the field by assessing the condition of sea-caught larvae.

MATERIALS AND METHODS

Jack mackerel eggs were collected by towing a 1-m (mouth diameter, 0.505-mm mesh) plankton net just below the sea surface at various locations between 20 and 200 mi (32 and 320 km) off the coast of southern California in June and July 1975 and in May 1976. The eggs were separated from most of the plankton at sea and then sorted by developmental stage at the Southwest Fisheries Center, La Jolla, Calif. Temperature was maintained at 15°C during sorting and in the larval rearing containers. The light cycle was 12 h light and 12 h dark. Five hundred normally developing eggs from a single day's spawning were transferred into 100 l black Kydex[2] circular rearing tanks containing filtered seawater (5 μm, Cuno filtered). There were three experiments and two treatments in each experiment; larvae in one tank were offered food while those in the other were not. The fed larvae were given a diet of a naked dinoflagellate, *Gymnodinium splendens* (50/ml), a rotifer, *Brachionus plicatilis* (30-40/ml), and a copepod, *Tisbe* sp. (1 or 2/ml). This feeding method has been described (Lasker et al. 1970; Theilacker and McMaster 1971; Hunter 1976b).

Histological criteria were developed in the first two experiments. The sampling procedure and the number of larvae sampled differed depending on the requirements of the analysis. Collectively, a total of 152 larvae were examined. In the third experiment, usually 15 larvae were sampled daily for 5 days from the "fed" tank (n = 69) and 3 days in the "starved" tank (n = 48). All larvae were examined both histologically and morphologically. No dead larvae were sampled because the postmortem change which takes place in tissues of fish larvae, due to digestion by their own enzymes (autolysis), resembled antemortem destruction caused by starvation. Standard length of each larva was measured on a slide; then seawater was removed and replaced by Bouin's fixative. Preserving individual larvae in this manner assured that each would be straight and flat, facilitating subsequent morphometric measurements. Five measurements were taken after preservation to monitor daily changes in larval body form and determine effects of starvation: standard length (SL, tip of upper jaw to tip of notochord), head length (HL, tip of upper jaw to cleithrum), eye diameter (ed), body depth at the pectoral (bd-1), and body depth at the anus (bd-2). Standard length shrinkage in Bouin's fixative was 11.5%. Next, measured larvae were prepared for histological examination using standard techniques. Larvae were transferred from Bouin's to 70% ethyl alcohol after 24 h, dehydrated with an ethyl n-butyl alcohol series in a Fisher Tissuemation, and embedded in Paraplast-plus. The Paraplast paraffin blocks were frozen with fluorocarbon spray (Cryokwick) just before the larvae were serially sectioned at 5 μm in a sagittal plane. The mounted sections were stained with Harris' hematoxylin and eosin and mounted in synthetic resin.

Histological Grading System

Recently O'Connell (1976) developed a numerical, histological grading system to characterize the nutritional condition of individual northern anchovy larvae. He examined tissues of the larvae microscopically to determine the features of tissue microstructure that were affected by starvation. A grade was assigned to each feature based on the degree of similarity or dissimilarity of the histological microstructure between the starved larvae and fed larvae. I followed this method and modified it as necessary for the tissues of jack mackerel.

Each of the histological characteristics used to assess starvation in jack mackerel larvae was evaluated and assigned a grade. A grade of "3" was given to a characteristic which resembled that in "normal or healthy" larvae, a grade of "2" was given to an intermediate condition, a grade of "1" to the starved condition. Since these criteria were established by comparing actively feeding, seemingly healthy larvae with moribund larvae, it was assumed that an average of the 12 graded features examined for each larva classified the larva into the correct nutritional group: "healthy group," average grade = 2.34 to 3.00; "intermediate group" = 1.67 to 2.33; and "starved" = 1.00 to

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

1.66 (the break points establish three equal groups).

Data Analysis

In the main, conclusions are based on the results of a stepwise discriminant analysis (SWDA). A discriminant analysis allows one to distinguish between two or more groups, given a set of variables that describe the characteristics in which the individuals in each group are expected to differ. In the stepwise discriminant analysis, all the variables are introduced into a SWDA computer program and the best set of variables, based on the generalized Mahalanobis distance (Rao 1952), is selected. The first variable chosen will usually be the one which gives the best score when classifying the individuals into their predetermined groups. The score is equal to the number correctly classified. The selection of each succeeding variable improves the score until a subset is chosen which is as good as the full set of variables for discriminating the groups. All variables not included in the final subset are considered superfluous, or not necessary for classification.

RESULTS

Histological

The histological condition of yolk-sac and actively feeding larvae ("normal") was compared with that of 3-day starved larvae and many differences were noted in the cells, tissues, and organs. The degree of apparent histological deterioration of 1- and 2-day starved larvae was intermediate between the "normal" and moribund status. This condition was termed "semi-starved" by Umeda and Ochiai (1975) and "intermediate" by O'Connell (1976).

The following section describes the normal histology of actively feeding jack mackerel larvae and that of starving larvae. Twelve histological criteria, which appeared to be indicators of starvation, were identified; they are numbered in the test below and are referenced in the photomicrographs (Figures 1-12).

Brain (Figures 3, 4)

The primitive brain cells exhibited a high incidence of mitotic activity (1) in normal larvae and there was relatively little intercellular space (2) between the round cells. In starved larvae, mitotic activity was arrested and many of the cells were shrunken, which caused large clear areas to appear between densely stained, atrophied cells.

Liver (Figures 5-8)

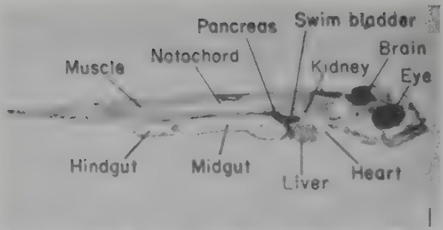
In the normal larval jack mackerel liver the hepatic cords were two cells thick. Within each hepatocyte, the nucleus (3) was regular in shape and distinct. The cytoplasm (4) was well dispersed with intracellular spaces, probably an area where glycogen and lipid are stored. Sinusoid areas, where metabolic exchanges take place between the hepatic cords, contained blood cells. After starvation for a few days, the liver atrophied, the cytoplasm condensed, stained darkly, and intracellular spaces had disappeared. There were focal degenerative or necrotic areas and accumulations of eosinophilic granules and masses. Nuclei were often irregular in shape and granules appeared around their periphery; these darkened areas are presumed to be condensed, inactive chromatin (Stein et al. 1975). The gallbladder (5) in starved larvae was always enlarged; normally it discharges its contents under the stimulus of food (Love 1970).

Pancreas (Figures 5-8)

Cells of the exocrine pancreas were arranged in series, in a circular fashion, as a secretory unit called an acinus. The nucleus (6), clear and distinct, was located in the basal portion of the pyramidal cells. The acinar arrangement of the pancreatic cells (7) was found to be very sensitive to deprivation of food. A breakdown in the symmetry in the acinus was slight but usually detectable after 1 day of starvation. Tissue degeneration after 3 days of starvation was extreme. The nucleus was irregular and uniformly stained and there was no detectable acinar arrangement. The presence of zymogen, digestive proenzyme secreted by the acinus and stored as granules at its central apex, was usually associated with starvation.

Digestive Tract (Figures 7-12)

The columnar epithelial cells of the midgut were closely united (8) in a single layer. Microvilli were visible along the border of the lumen giving a brush effect. In starved larvae, the midgut cells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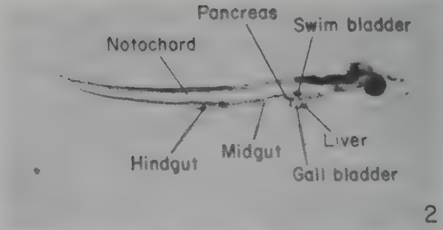
Swim bladder
Brain
Muscle
Notochord
Kidney
Eye
Hindgut
Midgut
Liver
Heart
1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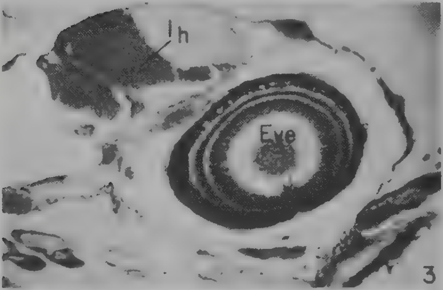
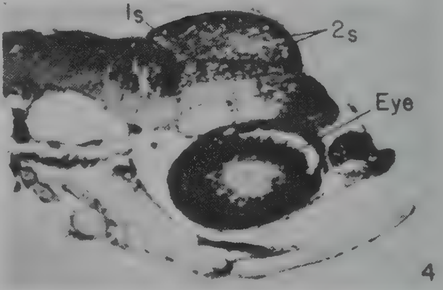
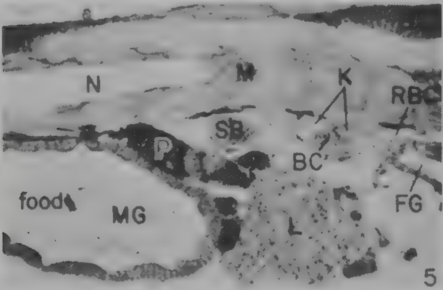
Swim bladder
Notochord
Liver
Hindgut
Midgut
Gall bladder
2



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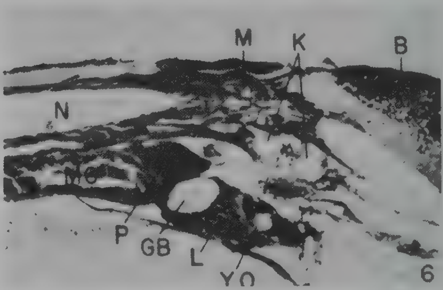
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FIGURE 1.—*Trachurus symmetricus* larva, day 8, fed for 3 days. All 12 histological criteria graded as "healthy." 32 ×.

FIGURE 2.—*Trachurus symmetricus* larva, day 8, starved for 3 days. All 12 histological criteria graded as "starved." 32 ×.

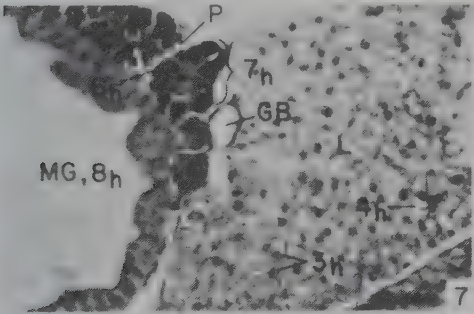
FIGURE 3.—Head of fed larva, graded "healthy." Mitotic activity (1 h) is indicated. Note close proximity of primitive brain cells to each other. 200 ×. h = histological grade = healthy.

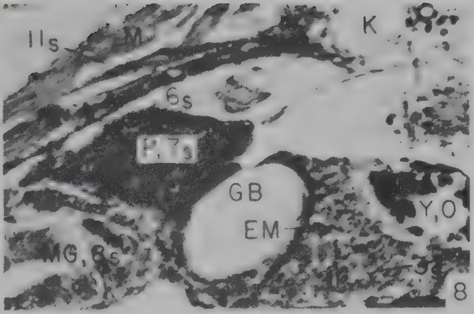
FIGURE 4.—Head of starved larva, graded "starved." Atrophied and darkly stained primitive brain cells (1 s); large intercellular spaces (2 s). 200 ×. s = histological grade = starved.

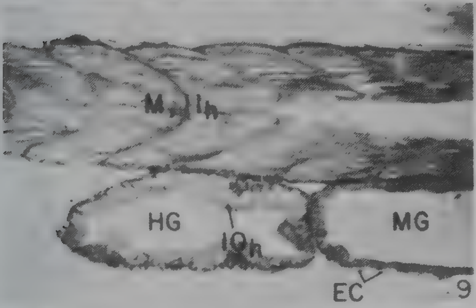
FIGURE 5.—Day 8 fed larva. Histological features graded "healthy." 200 ×. See enlargement, Figure 7. B = brain, BC = blood cells (white or immature red), FG = foregut, I = Islet of Langerhans (endocrine pancreas), K = kidney, L = liver, MG = midgut, M = muscle, N = notochord, P = exocrine pancreas, RBC = red blood cells, SB = swim bladder.

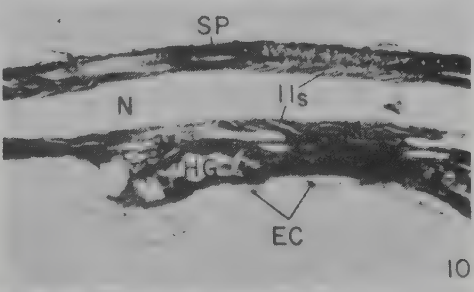
FIGURE 6.—Day 8, starved larva. Histological features graded "starved." 200 ×. See enlarge, Figure 8. GB = gallbladder, O = oil, Y = yolk, see Figure legend 5 for rest of symbols.

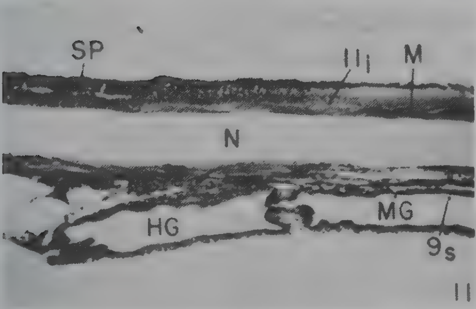
FIGURE 7.—Day 8 fed *Trachurus symmetricus* larva. Enlargement of Figure 5. Midgut cells in close union (8 h); prominent nuclei (3 h) and large intracellular spaces (4 h) in the liver; pancreatic nuclei distinct (6 h) and cells arranged in a circular unit (acinus) (7 h); gallbladder (GB) "normal." 480 ×. h = histological grade = "healthy," L = liver, MG = midgut, P = exocrine pancreas.











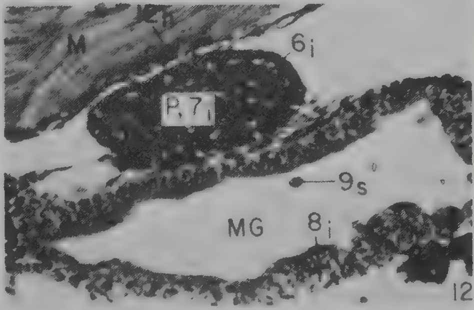


FIGURE 8.—Day 8, starved *Trachurus symmetricus* larva. Enlargement of Figure 6. Loss of integrity of midgut cells (8 s); atrophied liver with dark staining and irregular nuclei (3 s); no acinar cellular arrangement in pancreas (7 s); separated muscle fibers (11 s); swollen kidney (K); distended gallbladder (GB); note presence of yolk and oil (Y, O), and eosinophilic mass (EM) in liver. 480 ×. s = histological grade = "starved," M = muscle, MG = midgut, P = exocrine pancreas.

FIGURE 9.—Day 8 fed larva. Large eosinophilic inclusions in hindgut (10 h); muscle fibers closely packed (11 h); thin, epithelial integumental cells (EC) are prominent below gut and above trunk musculature. 200 ×. h = histological grade ="healthy," HG = hindgut, M = muscle, MG = midgut.

FIGURE 10.—Day 8, starved larva. Loss of cellular structure in hindgut; enlarged epithelial integument cells (EC); separated muscle fibers (11 s). 200 ×. s = histological grade = "starved," HG = hindgut, M = muscle, N = notochord, SP = spinal cord.

FIGURE 11.—Day 7 larva, starved 2 days and histologically graded "intermediate." No inclusions in hindgut; cellular separation in midgut (MG) and hindgut (HG); midgut cells sloughing (9 s); muscle fibers beginning to separate (11 i). 200 ×. i = histological grade = intermediate, s = histological grade = "starved," M = muscle, N = notochord, SP = spinal cord.

FIGURE 12.—Day 7 larva, starved 2 days, graded "intermediate." Abundant intermuscular tissue (12 h); no muscle (M) fiber separation; pancreatic nuclei (6 i) not distinct and cellular acinar arrangement lacking (7 i); midgut cells separating (8 i) and sloughing (9 s). 480 ×. i = histological grade = intermediate, s = histological grade = "starved," MG = midgut, P = exocrine pancreas.

began to separate from each other. It appeared that the midgut was extremely vulnerable to a deficiency of food and usually after 1 day of starvation, single mucosal cells could be seen sloughed (9) into the lumen. The margin of the lumen continued to lose its integrity as starvation advanced. Cells of the hindgut of feeding larvae exhibited an accumulation of eosin staining inclusions. The inclusion bodies, which may be the sites of intracellular digestion, have been observed in other marine and freshwater fish (Kostomarova 1962; Iwai and Tanaka 1968a, b; Iwai 1968; Umeda and Ochiai 1975; O'Connell 1976). The amount, size, and intensity of the staining (10) of these inclusions varied in feeding larvae. They were not present in starving larvae.

Musculature (Figures 9, 10, 12)

In feeding jack mackerel larvae, individual muscle fibers were close together (11); they were composed of closely packed, striated, and parallel myofibrils. After a period of starvation, the fibers separated, the fibrils were not distinct, and occasionally they lost their parallel structure. Between some fibers there was a granular, basophilic, nucleated substance called "intermuscular tissue" (12) by O'Connell (1976). In starved larvae, this tissue was usually absent.

General Histological Characteristics

After jack mackerel larvae had starved for 3 days, signs of depletion were widespread. In addition to changes in major tissues and organs there was a general atrophy and disintegration of all cells and tissues including those of cartilage, kidney, endocrine pancreas, and swim bladder. The number of pyknotic nuclei (i.e., darkening and shrinking nuclei, which give the first indication that a cell is dying) increased in all tissues (see eye and brain, Figure 4). Epithelial cells of the integument were hypertrophic, twice as large as normal in 3-day starved larvae (Figure 10), and kidney tubules were swollen (Figure 6). There was always a larger yolk reserve retained by starving larvae (Figure 6). A decrease in yolk absorption in starving larvae was also reported by Kostomarova (1962) for pike and carp and by Umeda and Ochiai (1975) for yellowtail.

Histological Grading

To determine whether the classification of a jack mackerel larva required the grading of all histological features or a lesser number, a group of 27 larvae, 14 feeding and 13 starving, was examined and the resulting grades for each criterion were submitted to a SWDA. The experimental treatment (fed or starved) was unknown until after all larvae were microscopically examined. The larvae were 7 days old and had been feeding or starving for 2 days. The grading system classified all fed larvae ($n = 14$) into the healthy group (individual average grade of the 12 histological features ranged between 2.42 and 2.92). The average grades for the 2-day starved larvae were more variable. The larvae were classified, about equally, into each of the three nutritional groups: four had a grade range between 2.35 and 2.54, ranking in the healthy group; four were classified as intermediate, grade range 2.08 to 2.31; and five larvae were ranked as starved with the average grades ranging between 1.15 and 1.54.

Results of the SWDA on the above data disclosed that grading only two histological characteristics, the arrangement of the cells in the pancreas (variable 7) and the sloughing of mucosal cells from the midgut (variable 9), gave the same conclusions as using all 12 features. Therefore, in all subsequent histological assessments, the average grade of these two criteria, variables 7 and 9, was used as the index of larval condition.

Morphological

The jack mackerel larvae were 2.45 mm SL (preserved) at hatching and initiated feeding at 3.35 mm, 5 or 6 days after hatching (hatching = day 0, Figure 13A). At the time of first feeding, some yolk and oil were present but the yolk sac was not discernible. The relationship between the five morphological characteristics, measured to determine the effects of starvation, and days of starvation is illustrated in Figure 13B-F. Since no data have been published on the daily growth rate of field-caught jack mackerel larvae, I used length as an estimate of age. When the morphometric measurements were plotted against length, no single measurement was a reliable index of starvation, as illustrated by pectoral body depth plotted for fed and starved larvae (Figure 14). However, some limits can be set from this graph: 1) all larvae <3.30 mm SL that do not have a yolk sac probably are starving (feeding is initiated at 3.35 mm); and 2) larvae with a body depth >0.47 mm are feeding. This leaves the size class between 3.30 and 3.55 mm where the cases cannot be separated. Most individuals in this class (29 fed and 24

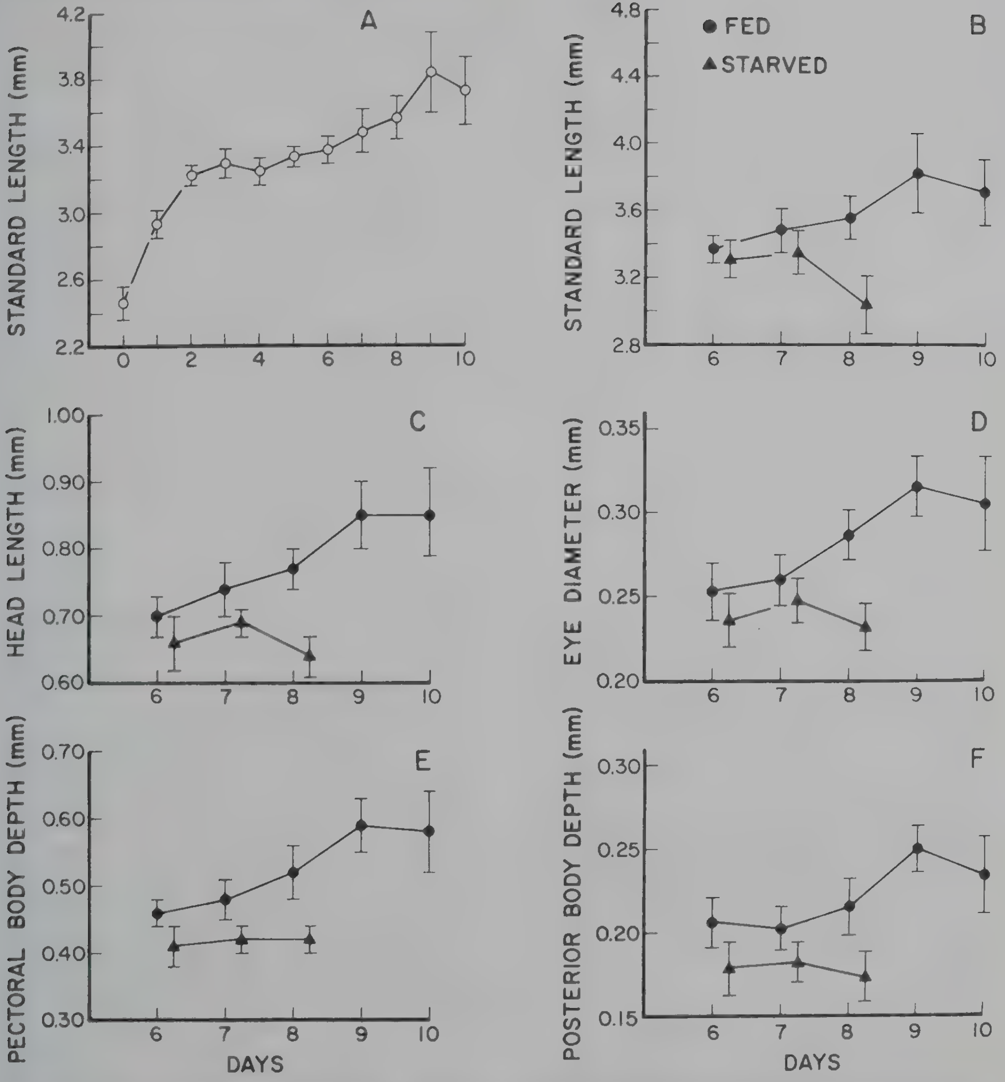


FIGURE 13.—A. Growth of *Trachurus symmetricus* larvae, with means and standard deviations. Sample size on any day was usually 15. B-F Relationship between five morphological characteristics of *T. symmetricus* larvae and days of starvation, with means and standard deviations. Sample size was usually 15.

starved) have been feeding or starving for 1 or 2 days.

To determine whether a set of several morphometric variables could predict the condition of larvae in the 3.30 to 3.55 mm size class, a SWDA was run. Eleven morphometric variables, in which the two predetermined groups (fed and starved) were expected to differ, were entered into the SWDA: 1) HL, 2) ed, 3) bd-1, 4) bd-2, 5) HL/SL, 6) ed/SL, 7) bd-1/SL, 8) bd-2/SL, 9) ed/HL, 10) bd-1/

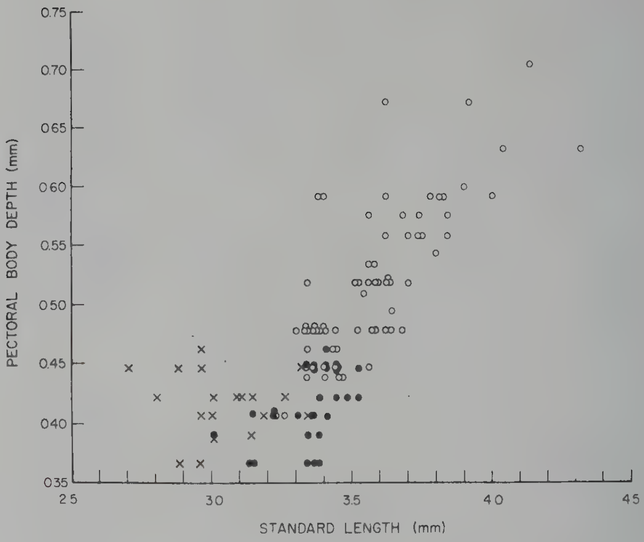


FIGURE 14.—Relationship between pectoral body depth and standard length of *Trachurus symmetricus* larvae which were fed (open circles), starved 1 and 2 days (dots), and starved 3 days (x's).

HL, and 11) bd-2/HL. Standard length was used in ratios and not as a unit to allow discrimination between fed and starved larvae of the same length. To discriminate between the two groups, the analysis selected a set of five variables, listed in the order of selection: 1) bd-2/SL, 2) bd-2/HL, 3) bd-1/HL, 4) ed/SL, and 5) bd-1. With these five variables, 83% of the fed and 86% of the starved larvae in the select size class were correctly classified. When all the larvae, 69 fed and 48 starved (Figure 14), were included in the analysis and the discriminant functions derived from the above five variables were used, 87% of the fed and 94% of the starved were correctly classified.

Comparison of Histological and Morphological Techniques

All larvae classified using morphometric characters were also analysed histologically (Table 1). The histological grading system classified 83% of the larvae which were fed into the healthy group and 83% of the larvae deprived of food for 3 days into the starved group. The histological grades of 1- and 2-day starved larvae were not as well defined; 19% of the cases were graded as healthy, 44% were graded intermediate, and 37% were graded starved. This outcome was similar to results of the initial histological study of 2-day starved larvae reported under Histological Results.

In the morphometric SWDA (Morphological Results), all the starved larvae (1-, 2-, and 3-day starved) were entered into the analysis as one group ($n = 48$). However, from the above histological grades of the starved larvae, the class should be divided into two groups, early starvation (including 1- and 2-day starved larvae which received all three histological grades) and prolonged starvation (including 3-day starved larvae which were mostly graded as starved). Preliminary laboratory experiments supported this decision. Food was offered to 1-, 2-, and 3-day starved larvae and some 1- and 2-day starved larvae did initiate feeding. No 3-day starved larvae ate food. The

TABLE 1.—Histological classification of *Trachurus symmetricus* larvae.

		Average histological grade		
Item	n	Healthy 2.34-3.00	Intermediate 1.67-2.33	Starved 1.00-1.66
Days fed:				
1	14	12	1	1
2	15	13	2	—
3	15	11	4	—
4	6	6	—	—
5	14	11	3	—
Days starved:				
1	13	3	5	5
2	14	2	7	5
3	18	2	1	15

feeding capability reported for other pelagic fish larvae, after an initial period of starvation, was similar to jack mackerel (Blaxter 1965; Lasker et al. 1970; May 1971). Because of these variables, the morphometric analysis was refined further to differentiate three groups.

Two methods of analyzing the morphometric data for three predetermined groups (fed, early starvation, and prolonged starvation) were examined using 1) all 11 variables previously described, and 2) the set of 5 variables chosen to discriminate between fed and starved larvae morphometrically. In the first test, the SWDA selects the best set of variables to discriminate between the three groups and in the second test, the analysis separates groups with a given set of variables.

The variables selected by the first test (in order of selection) were: 1) bd-2, 2) bd-2/SL, and 3) HL. The set of three variables correctly classified 84% of the fed larvae, 93% of the early starved larvae, and 79% of the prolonged-starved larvae (Test 1, Table 2). The inclusion of two more variables, bd-2/HL and bd-1/HL, did not improve the classification scores. The second test, using the previously chosen set of five variables, correctly classified 84% of the fed larvae, 90% of the early starved, and 74% of the prolonged-starved larvae (Test 2, Table 2). The first test had a better score for both the early and prolonged starvation groups, but either set of variables is a reliable predictor of larval condition.

TABLE 2.—Morphological classification of *Trachurus symmetricus* larvae. The number of larvae in the predicted groups (experimental conditions) is compared with the actual group membership determined by a stepwise discriminant morphometric analysis. Test 1 uses a set of three variables: posterior body depth, posterior body depth divided by standard length, and head length, and Test 2 uses a set of five variables: posterior body depth divided by standard length and head length, pectoral body depth divided by head length, eye diameter divided by standard length, and pectoral body depth.

Experimental conditions	*n*	Fed	Starved 1 and 2 days	Starved 3 days
		Group membership test 1		
Fed	69	58	10	1
Starved				
1 and 2 days	29	1	27	1
3 days	19	0	4	15
		Group membership test 2		
Fed	69	58	10	1
Starved				
1 and 2 days	29	2	26	1
3 days	19	1	4	14

Either the morphological or the histological technique can be used to identify fed larvae and 3-day starved larvae (Table 3). Fifty-three of the 64 (83%) larvae which were offered food were classified as fed (column 2) by the morphometric SWDA and as healthy (column 3a) by the histological method; but, only 44 of these larvae had the score in common (Table 3). Within the 3-day starved group, 14 of the 18 (78%) larvae were correctly classified (column 2) with the morphometric analysis and 15 (83%) were labelled correctly with the histological technique; 13 larvae had the starved score in common. It is difficult to compare the morphological and histological scoring of the early starvation (1- and 2-day starved) group. The morphometric analysis was extremely sensitive for selecting this group, 96% were correctly classified; however, the histological analysis may be more accurate for indicating which larvae in this group can still feed. Five of the 27 (19%) early starved larvae were histologically graded as healthy and may be capable of feeding. It is also possible that intermediate grade larvae (44%) would eat if exposed to food. Eleven of the 12 fish in this intermediate group had a score in common with the morphometric analysis. Intermediate larvae exhibit some tissue degeneration which may be reversible. Additional laboratory experiments are required to determine survi-

TABLE 3.—*Trachurus symmetricus* larvae were fed or starved for 1, 2, or 3 days (column 1). Each larva was classified with the morphometric method (column 2) and the histologic method (column 3). The percent of the larvae correctly classified with each method and the number of larvae correctly classified by both methods is also indicated.

Experimental conditions[1] (1)	Morphometric analysis (2)		Histological analysis (3) Healthy	Intermediate	Starved
		n	53/83%	10	1
Fed *n* = 64	Fed	53/83%	44	8	1
	Starved 1 and 2 days	10	8	2	0
	Starved 3 days	1	1	0	0
		n	5	12/44%	10
Starved 1 and 2 days *n* = 27	Fed	1	0	1	0
	Starved 1 and 2 days	26/96%	5	11	10
	Starved 3 days	0	0	0	0
		n	2	1	15/83%
Starved 3 days *n* = 18	Fed	0	0	0	0
	Starved 1 and 2 days	4	1	1	2
	Starved 3 days	14/78%	1	0	13

[1] The total number of larvae within each experimental group agrees with Table 1 but differs from Table 2 because several larvae were lost during the microtechnique procedure

val when feeding is only delayed for 1 or 2 days and to ascertain whether tissue degeneration noted during the period of early starvation is reversible.

DISCUSSION AND CONCLUSION

The effects of starvation could be seen throughout the body of larval jack mackerel. There was atrophy of all tissues, with the digestive tract and its associated glands the first tissues affected by starvation. The extent of cellular deterioration increased with time of starvation. Many histological changes, which were associated with starvation in jack mackerel, were similar to changes described in other starving fish larvae: 1) atrophy and cellular and nuclear degeneration of the liver (yellowtail, Umeda and Ochiai 1975; northern anchovy, O'Connell 1976; plaice, Karl Ehrlich pers. commun.), 2) separation of muscle fibers (northern anchovy, O'Connell 1976; herring and plaice, Ehrlich pers. commun.), 3) cellular and nuclear degeneration in the pancreas (yellowtail, Umeda and Ochiai 1975; northern anchovy, O'Connell 1976), and 4) decrease in the size of the epithelial cells in the digestive tract (pike and carp, Kostomarova 1962; yellowtail, Umeda and Ochiai 1975; herring and plaice, Ehrlich et al. 1976; northern anchovy, O'Connell 1976). Some histological changes present in starved jack mackerel larvae, enlargement of the gallbladder and deterioration of the primitive brain cells, have not been reported for other starved fish larvae.

The onset of starvation in jack mackerel larvae was manifested as 1) a change in acinar arrangement of the pancreatic cells and 2) a sloughing of mucosal cells from the midgut into the lumen. These two criteria were shown to be critical variables and were histologically graded to assess the nutritional condition of jack mackerel larvae. O'Connell (1976) reported that the condition of the pancreas was of primary importance for classifying starving northern anchovy larvae. His criteria for good pancreatic condition depended on the abundance of zymogen as well as continuity of cellular structure. The presence of zymogen was not used as a criterion to classify jack mackerel larvae; absence of zymogen was usually associated with feeding, however, the correlation was not consistent. O'Connell also noted mucosal cells in the midgut of larval anchovy but he did not grade this feature. Love (1970) suggested that sloughed midgut cells may be used as an energy source.

During starvation, growth was retarded, larvae shrank, and the soft tissues collapsed causing larvae to look abnormal; the body became bent and thin and the head disproportionately large. An array of larval fish morphometric characteristics have been associated with nutritional condition. A decrease in depth of the larval body has been considered to be an important indicator of starvation although Blaxter (1971) did not find it to be a sensitive character for elongate clupeoid larvae. However, body depth divided by standard length appears to reflect the condition of postlarval anchovy (Nakai et al. 1969) and older, larval northern anchovy (Arthur 1976), but the ratio did not identify feeding and starving post yolk-sac northern anchovy (O'Connell 1976). Nakai et al. (1969) also related the diameter of the posterior digestive tract to condition in postlarval anchovy. The height of the body in the posterior part of the trunk was measured by Honjo et al. (1959) and was found to differ between postlarval anchovy collected from two fishing grounds. Honjo et al. (1959) suggested that the anatomical difference was indicative of a higher availability of food organisms in one area than in the other. Another predictive parameter for the condition of post yolk-sac larvae was the relative condition factor reported by Ehrlich et al. (1976) for herring and plaice. Its estimation involves weighing each larva. All of the above mentioned morphological criteria reflect larval nutritional condition and may be considered reference parameters, but no one criterion accurately identifies larval condition on an individual basis. The lack of sensitivity of a single morphometric indicator may be due to natural variability alone or more probably to the rapid morphological changes which occur in larval fish. For example, Zweifel[3] using the data of Hunter (1976b) has shown that for feeding northern anchovy larvae the condition factor weight/length^3 was neither constant nor monotonic even when food densities were carefully controlled. For variation in food levels (including no food) it would be expected that there should be even more complex relationships.

Even though the histological and morphological techniques have proven to be effective for predicting condition of laboratory-reared animals, both techniques must be field tested with wild-caught larvae. Evidence of morphological differences between laboratory-reared and sea-caught larvae indicates that it may be difficult to transfer laboratory results to the sea. Blaxter (1968, 1971), for example, found laboratory-reared herring larvae exhibited a greater size variation and a higher condition factor than sea-caught larvae. Balbontin et al. (1973) reported differences in body depth, head depth, and head length between laboratory and wild herring juveniles of the same length. The laboratory-reared animals had a deeper body and a deeper or longer head.

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[3] Zweifel, J. 1977. A non-linear model for allometry in larval fish. Unpubl. manuscr., 25 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

The usefulness of the morphometric discriminant technique will depend upon the consistency of changes in morphological pattern in individuals when feeding and starving. However, even if the changes are not constant, useful indicators of larval survival will not require the exact allocation of all individuals into feeding and starving groups but rather only reasonable estimates of the relative proportions will be needed. My results indicate that a multivariate statistical approach, combining several morphometric measurements in a SWDA, may provide this information. Species that do not yield to a morphological analysis should yield to the histological approach.

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THE FISH RESOURCES OF THE WESTERN CENTRAL PACIFIC ISLANDS

by

Richard N. Uchida
Southwest Fisheries Center
National Marine Fisheries Service
Honolulu, Hawaii 96812
USA

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ROME, June 1978

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CONTENTS

Page

1. TOPOGRAPHY 1

2. HYDROGRAPHY 1

2.1 Surface currents 1
2.2 Surface temperature 3
2.3 Thermocline 4
2.4 Surface salinity 4
2.5 Upwelling 5
2.6 Undercurrent 5

3. PRIMARY PRODUCTION 6

3.1 Oceanic regions 6
3.2 Coral reef 8

4. ZOOPLANKTON 8

5. BENTHOS 10

5.1 Coral reefs 10
5.2 Other shallow-water areas (less than 200 m) 10
5.3 Deep to very deepwater areas 11

6. FISH STOCKS AND FISHERIES 12

6.1 The fisheries 12

6.1.1 American Samoa 12
6.1.2 Cook Islands 13
6.1.3 Fiji Islands 13
6.1.4 French Polynesia 14
6.1.5 Gilbert Islands 14
6.1.6 Guam 14
6.1.7 Hawaiian Islands 15
6.1.8 Nauru 16
6.1.9 New Caledonia and dependencies 16
6.1.10 New Hebrides 17
6.1.11 Niue 17
6.1.12 Papua New Guinea and West Irian 17
6.1.13 Solomon Islands 18
6.1.14 Tokelau Islands 19
6.1.15 Tonga Islands 19
6.1.16 Trust Territory of the Pacific Islands 20
6.1.17 Tuvalu 20
6.1.18 Wallis and Futuna Islands 20
6.1.19 Western Samoa 20

6.2 Statistics 21
6.3 Stock assessment 22

6.3.1 Anchovy, *Stolephorus purpureus* and *S. heterolobus* 26
6.3.2 Bigeye scad, *Trachurops crumenophthalmus* 27
6.3.3 Pelagic armorhead, *Pentaceros richardsoni* 27

CONTENTS (cont.)

Page

6.4 Other estimates of potential: Fishing surveys and exploratory fishing 27

6.4.1 American Samoa 27
6.4.2 Cook Islands 27
6.4.3 Fiji Islands 27
6.4.4 Hawaiian Islands 28
6.4.5 Line Islands 31
6.4.6 New Caledonia 32
6.4.7 Papua New Guinea 32
6.4.8 Solomon Islands 32
6.4.9 Tonga Islands 32
6.4.10 Trust Territory of the Pacific Islands 33
6.4.11 Tuvalu 33
6.4.12 Wallis and Futuna Islands 34
6.4.13 Western Samoa 34

6.5 Crustaceans 35

6.5.1 Frog crab 35
6.5.2 Spiny lobsters 36
6.5.3 Shrimp 38

6.6 Molluscs 38
6.7 Echinoderms 39

7. CIGUATERA 40

8. DISCUSSION 42

9. REQUIREMENTS FOR FURTHER STUDY 43

10. REFERENCES 43

1. TOPOGRAPHY

As defined here, the western central Pacific islands include American Samoa, Cook Islands, Fiji Islands, French Polynesia composed of the Austral, Gambier, Marquesas, Rapa, Society, and Tuamotu Islands, Gilbert Islands, Guam, Hawaiian Islands, Line Islands, Nauru, New Caledonia, New Hebrides, Niue, Papua New Guinea, Solomon Islands, Tokelau Islands, Tonga Islands, Trust Territory of the Pacific Islands, Tuvalu, Wallis and Futuna Islands, and Western Samoa.

Around these islands, there is little or no shelf area, which along the continents supports large-scale trawl fisheries for various demersal species. Usually, the bottom contour near the coast is highly irregular and drops off precipitously to deep water several kilometers beyond the outer reef.

Data on bottom topography are rather sparse for the islands of the western central Pacific. For Fiji Islands, the shelf area to 200 m is estimated to be 15,000 km^2 (FAO 1972), whereas off Western Samoa, the shelf area is 4,500 km^2 (FAO 1975b). Off the Solomons, which has a coastline totaling 4,023 km, the shelf area is about 100,000 km^2 (Moiseev 1969). The shelf area to a depth of 914 m around the major Hawaiian group (Hawaii to Kauai) is estimated to be about 44,076 km^2 (Yoshida 1972).

2. HYDROGRAPHY

2.1 Surface currents

Two regions of trade wind induced currents, one in each hemisphere, exist in the Pacific Ocean. These currents have a persistent westward drift during the entire year. The tangential stress of the persistent trade winds, which embrace the major part of the world's ocean, is responsible for the trade wind regions being the center of action for surface circulation (Dietrich 1963).

In the western central Pacific, the dominating influence is the North and South Equatorial Current. The major oceanic circulation in the Pacific is shown in Figure 1.

Because the thermal Equator remains in the Northern Hemisphere throughout the year, the North and South Equatorial Currents are not symmetrical about the geographical Equator (Defant 1961). The southern boundary of the North Equatorial Current is between lat. 6° and 7°N in winter and between lat. 9° and 11°N in summer. The current, which is much stronger in winter, increases its velocity steadily toward the western Pacific. Wyrtki (1967) estimated that the North Equatorial Current has surface velocities of about 25 cm/sec near the northernmost part, up to 32 cm/sec near lat. 15°N, and in excess of 42 cm/sec near the southern boundary. The net transport in the North Equatorial Current is about 22 million m^3/sec. Off the Philippines, the North Equatorial Current divides into two branches; one flowing northward to become the Kuroshio and the other turning southward into the Equatorial Countercurrent (Defant 1961).

The South Equatorial Current, which extends the width of the southeast trade wind belt between lat. 5°N and 40°S, has its highest velocity and constancy along the northern boundary between lat. 5°N and 5°S (Defant 1961). West of Papua New Guinea and the Solomons, the South Equatorial Current is strongly developed during the northern summer and extends as far as Halmahera. It flows along the north coast of Papua New Guinea, into the Southeast Asian region south of Mindanao and Halmahera, then recurves northward and eastward to become the principal water mass of the countercurrent. Off east Australia, the South Equatorial Current bends southward to become the East Australian Current. The South Equatorial Current is broken near lat. 10°S by the eastward flowing South Equatorial Countercurrent (Reid 1959).

The flow representing the northern part of the South Equatorial Current has geostrophic speeds exceeding 110 cm/sec. The net transport between lat. 6°N and the Equator

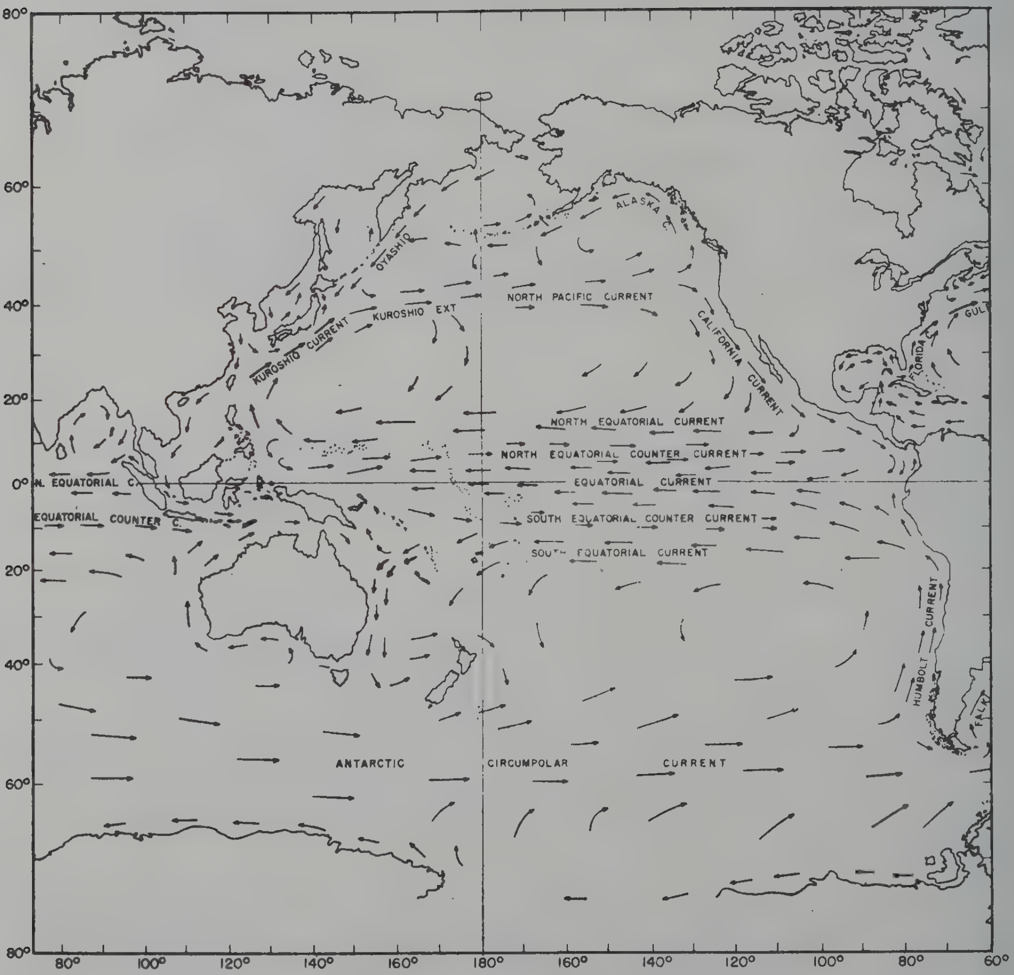
80°
60°
40°
20°
0°
20°
40°
60°
80°
ALASKA C.
OYASHIO
NORTH PACIFIC CURRENT
KUROSHIO EXT
KUROSHIO CURRENT
CALIFORNIA CURRENT
GUL
FLORIDA
NORTH EQUATORIAL CURRENT
NORTH EQUATORIAL COUNTER CURRENT
N. EQUATORIAL C.
EQUATORIAL CURRENT
EQUATORIAL COUNTER C.
SOUTH EQUATORIAL COUNTER CURRENT
SOUTH EQUATORIAL CURRENT
HUMBOLT CURRENT
FALK
ANTARCTIC
CIRCUMPOLAR
CURRENT
80°
100°
120°
140°
160°
180°
160°
140°
120°
100°
80°
60°

Figure 1.--Major features of the surface circulation of the Pacific Ocean (McLellan 1965).

is 32 million m^3/sec to the west, indicating that the South Equatorial Current is well developed (Montgomery and Stroup 1962).

Between the North and South Equatorial Currents, the countercurrent exists all year long (Defant 1961). During the northern winter, the countercurrent is weak and narrow except near its origin in the west; however, during the northern summer, particularly in August-September, the countercurrent flows persistently from Mindanao-Palau-Halmahera to Panama, a distance of nearly 15,000 km. The countercurrent, which extends about 550 km in width between lat. 5° and 10°N, is separated from the two Equatorial Currents on both sides by well-defined boundaries, particularly on the northern side.

In the countercurrent, the velocity distribution shows a subsurface velocity maximum, which coincides approximately with the lower boundary of the thermocline and has speeds in excess of 60 cm/sec to the east. Below 200 m, the flow is westward, thus showing that the countercurrent is limited to a shallow surface layer. The net transport is estimated to be 26 million m^3/sec in the 0-500 m depth range.

2.2 Surface temperature

Monthly mean, minimum, and maximum sea-surface temperatures may be found in LaViolette (1970). Table 1, which shows the mean annual sea-surface temperatures for the Pacific for 10° zones of latitude, indicates that the thermal Equator is displaced northward; the temperature maximum lies at about lat. 7°N. Particularly noticeable is the large contrast between the North and South Pacific in sea-surface temperature; in the Northern Hemisphere, the temperature usually is about 1°-2°C warmer in all latitudes.

Table 1.--Mean annual sea-surface temperature for 10° latitudinal zones (°C) (Defant 1961).

Latitude	North Pacific Ocean	South Pacific Ocean
0°-10°	27.2	26.0
10°-20°	26.4	25.1
20°-30°	23.4	21.5
30°-40°	18.6	17.0
40°-50°	10.0	11.2
50°-60°	5.7	5.0
60°-70°	--	-1.3
70°-80°	--	-1.7

In November-April in the North Pacific, north of the Hawaiian chain, a latitudinally parallel isothermal structure exists which has a temperature gradient of about 0.6° to 0.8°C per degree of latitude (Seckel 1962). A change in this temperature structure first becomes apparent in May followed by a breakdown of the parallel isothermal structure in June. An irregular temperature regime persists in the northern section of the Hawaiian chain in July-September, but in October, the isotherms again become parallel.

Minimum and maximum temperatures generally occur in March and September, respectively (Seckel 1962). Although the minimum sometimes occurs in February and the maximum in August or October, they show no significant differences from those in March and September.

West of the Hawaiian Islands, in the region of Micronesia, surface temperatures show small variations throughout the year (LaViolette and Seim 1969). In the Marshalls, surface temperatures vary between 23° and 33°C; the lows usually occur in March-April and the highs in September-October. Around the Western Carolines and Marianas, the minimum temperature is about 24°C and the maximum slightly above 29°C. Temperatures are usually lowest in February and highest in August-September. One of the notable features of the surface temperatures around the Marshalls is that it usually decreases slowly with increasing latitude (Mao and Yoshida 1955). In summer, low-surface temperatures occur at or near the Equator indicating intense upwelling associated with equatorial divergence. In the winter, however, the feature is not evident.

2.3 Thermocline

The main or permanent thermocline is always present in the Hawaiian region (Seckel 1962). Below the mixed layer, the average temperature gradient is about 15°, 6°, and 5°C per 100 m at lat. 10°, 20°, and 30°N, respectively. Superimposed on the permanent thermocline may be a seasonal thermocline and, in addition, there may also be a diurnal thermocline, which is defined as a small rise in surface temperature of the order of 1°C extending to a depth of about 10 m.

In the central Pacific, the mixed surface layer is uniformly warm; a few patches of water above 26°C appear in the countercurrent and South Equatorial Current (Wyrtki 1967). The thermocline in the North Equatorial Current between lat. 19° and 9°N varies from 100 to 200 m but deepens to the south. Between lat. 9° and 5°N, where the countercurrent flows, the thermocline is very steep and isotherms between 12° and 24°C are closely spaced. The Equatorial Undercurrent is very pronounced and is characterized by a spreading of the isotherms within the thermocline.

At long. 137°E, the depth of the main thermocline slopes sharply downward from the northern edge of the Kuroshio to the southern edge, where the mixed layer is nearly isothermal and thickest over the section. Southward from lat. 30° to 15°N, the thermocline shallows gradually. The thermocline is shallowest and the vertical temperature gradient largest at the boundary between the North Equatorial Current and the countercurrent (Masuzawa 1967).

2.4 Surface salinity

Equivalent to temperature in importance as a climatic indicator in oceanography is salinity. In the vicinity of the Hawaiian Islands, the maximum surface salinity occurs in November-February and the minimum in July (Seckel 1962). The 35°/oo salinity isopleth moves northward in April, reaches an extreme position in July, then moves southward and eventually positions itself at lat. 17°-19°N, the extreme winter location, in November-February. The maximum surface salinity of 35.35°/oo is reached at lat. 28°N. The high salinity gradient found within and slightly north of the Hawaiian chain indicates the presence of a transition zone or boundary between different types of water.

To the north and south of the Hawaiian Islands, low and high salinities occur about the same time as low and high temperatures (Seckel 1962). In the vicinity of the Hawaiian Islands, however, low and high salinities occur about 3 mo after the time that the mixed layer reaches its minimum and maximum depths, respectively. Near Midway, where the salinity maximum is located, a sharp decline of about 0.35°/oo is evident, resulting from either a southward or a northward displacement of the high salinity cell.

From the Hawaiian Islands southward, surface salinity decreases and the lowest values (less than 34.1°/oo) are observed in the North Equatorial Current between lat. 14° and 9°N (Charnell, Au, and Seckel 1967a, 1967b, 1967c, 1967d, 1967e, 1967f; Wyrtki 1967). Between the North Equatorial Current and the countercurrent at about lat. 9°N, a salinity front marks the boundary between low-salinity tropical surface water and high-salinity equatorial water. In the southern portion of the countercurrent and the northern part of the South Equatorial Current, in which the equatorial surface water lies, salinities are about 34.8°/oo. Just north of the Equator at lat. 0°31'N, another front in surface salinity is apparent. Here, equatorial surface water of about 34.8°/oo is separated from subtropical surface water of the South Pacific. Both salinity fronts, however, do not coincide with current boundaries.

From north to south, across the countercurrent and into the South Equatorial Current, the salinity ranges between 34.0°/₀₀ at lat. 10°N and 35.2°/₀₀ near the Equator (Austin 1960). Somewhat farther south and east of the Line Islands is the southeastern Pacific surface salinity maximum of 36.0°/₀₀ or greater.

In the western equatorial Pacific, a notable feature of the horizontal distribution of salinity is the separation of the northern and southern high-salinity regions by one of low salinity, usually located between the Equator and lat. 10°N. The low-salinity water which intervenes between the northern and southern tropical waters is also tropical water which may have been transported westward from the eastern Pacific. The east Indian Ocean is another source of low-salinity tropical water which apparently flows through the Molucca Passage (Cannon 1966).

In the Western Carolines along long. 137°E, the North Pacific tropical water with salinity exceeding 35°/₀₀ lies in the upper part of the thermocline between lat. 10° and 20°N and is in contact with the sea surface near lat. 19°N. Saline water originating in the South Pacific is also detected in the Western Carolines and extends as far north as lat. 6°N near the northern boundary of the countercurrent. The North Pacific major salinity minimum can be traced from the coast of Japan as far south as lat. 15°N (Masuzawa 1967).

The most outstanding feature of the horizontal distribution of salinity in the Marshalls is the presence of a low-salinity band in the region between lat. 5° and 10°N where large eddies exist (Mao and Yoshida 1955). Waters of high salinity push toward this band of low salinity from both sides. The gradient on the southern side suggests that the strongest influx of high-salinity water comes from the Southern Hemisphere.

The band of low-salinity water results from high precipitation, absence of saline tropical water from the north and south at these latitudes, ascent of the northern intermediate water mass with decreasing latitude, and upwelling associated with currents and eddies. Upwelling, which originates at some intermediate depth, brings cool, low-salinity water into the upper level. The ascending northern and southern intermediate water masses may further strengthen this upwelling.

2.5 Upwelling

In the central Pacific, there is a zone of horizontal divergence and an adjacent zone of convergence near the Equator. The boundary between north-south convergence and divergence, shifts latitudinally depending on wind direction. The divergence feature of Cromwell's (1951, 1953; Sette 1955) model explained the equatorial upwelling whereas convergence produced significant sinking.

Briefly, the model proposed that under the stress of easterly winds, surface water moves in a westerly direction at the Equator, but Coriolis force north and south of the Equator tends to deflect the surface water poleward. As the water moves away from the Equator, deeper water rises toward the surface. When there are northerly or southerly components in the easterlies, asymmetry is introduced and the center of upwelling is displaced. For example, southeast trades would displace the center of upwelling to the south of the Equator.

North of the Equator, convergence occurs as the denser upwelled water sinks between the center of upwelling at the Equator and the southern edge of the low-density water of the countercurrent which flows from west to east. At deeper levels, sinking water may turn southward thus completing a cell, or it may move northward and dive under the countercurrent.

2.6 Undercurrent

The first clue to the existence of a submerged current near the Equator was provided through observations on the drift of longline fishing gear in the central equatorial

Pacific. The longline gear, suspended from buoys and floating freely in the water, has the main mass of fishing lines about 150-180 m below the surface (Cromwell, Montgomery, and Stroup 1954). Set near the Equator a number of times during exploratory fishing cruises, the gear moved eastward in spite of opposing trade winds, currents, and seas at the surface. This suggested that a submerged current was prevalent near the Equator. The existence of this eastward moving current in the lower part of the surface layer and upper thermocline was proved by using surface and deep drags.

3. PRIMARY PRODUCTION

3.1 Oceanic regions

Primary production of 5-10 mg C/m^3/day (average 6.7 mg C/m^3/day) is characteristic of the oceanic zone of not only the boreal and Antarctic regions but also of areas with less intense ascent of deep waters near the equatorial region (Koblentz-Mishke 1965). A narrow band of water in temperate latitudes and a broader one around the Equator have productivity at the surface varying between 2 and 5 mg C/m^3/day (3.8 on the average) and which may provisionally be referred to as transition zones. Low productivity, averaging 1 mg C/m^3/day, is restricted to extensive areas of tropical waters mainly occupied by the northern and southern central water masses.

In the central Pacific, the area of highest primary production is in waters of the countercurrent (Bogorov 1960a, 1960b). Bogorov characterized the different types of water in the central Pacific as shown in Table 2.

Table 2.--Physical, chemical, and biological characteristics of the geographical water zones established for the central Pacific Ocean (Bogorov 1960a).

Zone	Temperature °C			Transparency, m	O_2 (ml/liter, at 0 m)	P-PO_4 (mg/m^3 at 0 m)	P-PO_4 (mg/m^3 at 100 m layer)	Number of bacteria per 50 ml	Number of phyto-plankton cells (m^3)	Biomass of zooplankton (mg/m^3)	Biomass of fish (mg/m^3) (1,000-0 m)	Benthos (mg/m^2)	Benthic sediments (g/cc)
	Air	Water											
		0 m	300 m										
Northern[1] subtropical	17.0	21.0	13.0	32	5.0	3.2	12.5	18	3,600	97	2.0	500-100	1.46
Northern equatorial	25.5	27.6	14.0	36	4.6	2.3	3.0	72	3,100	26	0.7	50	1.40
Equatorial counter-current	27.5	29.1	10.9	26	4.1	9.0	14.0	150	19,900	46	1.4	50	0.90
Southern equatorial	27.0	28.4	14.5	38	4.4	8.0	10.0	95	4,300	12	0.7	50	1.00
Southern subtropical	22.0	21.7	15.0	39	5.5	4.9	7.1	38	3,600	36	1.2	160-400	1.20

[1] The characteristics of the subtropical zones are presented as a mean of the values of the northern and southern portions of these zones.

Dividing the northern subtropical zone water into a northern section along lat. 40°N and a southern section along lat. 30°N, Bogorov found that in the northern section, phosphate is low at the surface but relatively high at deeper levels. The bacterial count per 50 ml and cell count of phytoplankton per cubic meter are relatively low. Here, diatoms predominate over peridinians in the phytoplankton samples. Along the southern section of this zone, phosphates and bacterial counts do not differ markedly from those values found for the northern section. The phytoplankton count, in which peridinians predominate, rises significantly to about four times the level encountered in the northern sector. Venrick (1974) observed that localized blooms of phytoplankton in this zone are dominated by an increase in the abundance of Rhizosolenia.

The water of the north equatorial zone at lat. 10°-12°N is relatively low in phosphate but moderately high in bacteria. The phytoplankton, composed primarily of peridinians, is somewhat lower than in the northern subtropical zone.

In the countercurrent zone, phosphates reach their highest levels in the surface layer. Also, more bacteria and phytoplankton occur here than in any other zone. The phytoplankton count shows an almost equal number of diatoms as peridinians.

At lat. 10°S where the southern equatorial zone is located, the water is relatively high in phosphate, moderate in bacteria, and sparse in phytoplankton. Bogorov observed that whereas peridinians predominate over diatoms at long. 174°W, their roles are reversed at long. 172°E.

The southern subtropical zone is also subdivided into a northern and southern section. The northern section at about lat. 20°S is characterized by water which is low in phosphate, bacteria, and phytoplankton and where peridinians predominate. At lat. 30°S, the southern sector of the southern subtropical zone has water moderately high in phosphate. The bacterial and phytoplankton counts, however, are considerably lower than in the northern sector of this zone.

In general, heterotrophic bacterial counts are low in the northern parts of the area surveyed, but increase sharply in the equatorial countercurrent zone where primary production is maximal (Bogorov 1960b). The usual picture is a predominance of diatoms over peridinians in high latitudes and vice-versa in the lower ones. This is supplemented by the result in the equatorial countercurrent zone where Bogorov found that the increase in phosphates was accompanied by a similar increase in algae. In the southern subtropical zone, the blue-green algae occupy a significant position in the composition of the phytoplankton.

Primary productivity in the western Pacific has been investigated by Sorokin (1973a, 1973b) and Sorokin and Tsvetkova (1972). Briefly, the studies revealed that bacterioplankton can serve as a large supplementary source of food for filter-feeding zooplankton, particularly in waters of maximum zooplankton concentration. This situation is typical in tropical regions where bacterial production may be twice the primary productivity through photosynthetic processes (Sorokin 1973a).

In the tropical western Pacific near the Solomon Islands, primary production on the surface measured by Koblentz-Mishke et al. (1977) was 0.4 and 1.0 mg C/m^3/day at two locations in waters of the South Equatorial Current, which is relatively poor in plankton, 3.0 mg C/m^3/day in the divergence zone of the Coral Sea, which is relatively rich in plankton, and 6.9 mg C/m^3/day in Kieta Bay of Bougainville Island. Sorokin and Tsvetkova (1972) determined also that primary production was higher near the equatorial divergence and lower along the convergence near lat. 12°N. Peak concentration of live phytoplankton is usually found at the upper boundary of the thermocline where the amount of nutrient salts is close to the level which limits phytoplankton development. The peak layer, according to Sorokin and Tsvetkova, is stable throughout the day.

For Ninigo and Admiralty Islands and Papua New Guinea, the thickness of the euphotic zone in the neritic area is 1.3 to 2 times that in the open ocean. In the lagoons, photosynthetic production is 12-14 mg C/m^3/day, but in one bay, which had a production of 39 mg C/m^3/day, photosynthesis takes place even at depths of 75 m with 10% of the light intensity at the surface (Sorokin 1973b).

3.2 Coral reef

Coral reefs, whether they are fringing shore reefs, barrier reefs that encircle the islands, or coral atolls, are one of the outstanding features within the western central Pacific. Coral reef communities are tremendously varied associations of plants and animals and are most noteworthy for their immense concentration of life and its complexity. That gross primary productivity or the rate of formation of organic matter can be very high in a coral reef environment is attributable to the recycling of nutrients within the system. The output of harvestable protein, however, is not particularly high (Clutter 1972).

Odum and Odum (1955), who determined the relationship between standing crop (dry biomass of existing organisms per area) and productivity (rate of manufacture of dry biomass per area), observed that in a windward coral reef community on Enewetak atoll, the average living coral colony contains three times as much plant as animal tissue or 0.063 g/cm^2 dry weight of algae as compared with 0.021 g/cm^2 of animal polyp. Zooxanthellae (in the coelènterate polyp) comprises roughly 6% of the total plant portion, whereas filamentous green algae embedded in the skeleton make up the bulk of the plant material. The study demonstrated that the algal-coelenterate complex comprises a highly integrated ecological unit, which permits recycling of food and nutrients necessary for vigorous coral growth in tropical "desert" waters of a low plankton content. The coral reef, therefore, is thought of as almost a whole ecological unit in itself including producers, herbivores (utilizing food from symbiotic algae), and carnivores (plankton feeding at night).

The study also revealed that in all zones of the reef, a trophic structure with a pyramid of biomass exists. For example, the mean standing crop for the reef as a whole is 703 g/m^2 for producers, 132 g/m^2 for herbivores, and 11 g/m^2 for carnivores. The ratio between standing crop trophic level for producer/herbivore is 5.3:1 and for herbivore/carnivore is 12:1. Based on these results, Odum and Odum (1955) estimated a very high total production rate of about 83 MT (metric tons)/ha, which represents a turnover (ratio of annual primary production to average standing crop) of about 12.5 times per year.

Reefs are also important to ocean production because the coastal fauna, which develops as an indirect result of the infusion of mineral salts from land and upwelling of nutrient-rich waters along the coast, enriches the pelagic sphere (Grandperrin 1977). This permanent infusion of coastal fauna from reef ecosystems in many Pacific islands represents a substantial biomass, which includes the larvae of drifting benthic species and meroplanktonic organisms (larvae of benthic organisms which have a free-swimming pelagic phase). In examining the stomach contents of pelagic, deep-swimming species caught far from the coast, Grandperrin found that of the total number of fish consumed by albacore, *Thunnus alalunga*, and yellowfin tuna, *T. albacares*, 58% and 73%, respectively, are regarded as coastal species. In bigeye tuna, *T. obesus*, however, coastal fishes are entirely absent.

4. ZOOPLANKTON

In the Pacific, zooplankton volume is distributed in a similar fashion as PO_4-P (Reid 1962). Volumes are usually high in the eastern boundary current, low in central water, and relatively high along the Equator and in two zones associated with equatorial divergence north and south of the Equator.

The biomass of zooplankton in the various geographical zones established by Bogorov (1960a, 1960b), for the central Pacific is given in Table 2. From north to south, Bogorov observed that the zooplankton biomass reaches 161 mg/m^3 in the northern sector of the northern subtropical zone but is only 34 mg/m^3 in the southern sector. In the equatorial zone, zooplankton is even more sparse, reaching only 26 mg/m^3. This sparseness is attributed to the depletion of nutrients as the water flows under the influence of the trade winds from the eastern to the central Pacific.

In the countercurrent zone, upwelling of deep water to the surface occurs over an enormous area enriching the photosynthetic zone (0-200 m) in phosphates and nitrates. As a result, zooplankton volumes reach 46 mg/m^3 in this zone.

In the Southern Hemisphere, Bogorov observed that the equatorial zone, unlike its counterpart in the Northern Hemisphere, is even more sparse in zooplankton, with volumes reaching only 12 mg/m^3. The zooplankton biomass then rises to 28 mg/m^3 in the northern sector of the subtropical zone and finally reaches 45 mg/m^3 in the southern sector.

Near the Line Islands, King and Demond (1953) observed that in the northern summer, the standing crop of zooplankton reaches a maximum of more than 50 cc/1,000 m^3 of water strained at lat. 2°C and long. 150°W near Palmyra. In the northern winter, the location of maximum abundance remains the same, but the standing crop is only between 25 and 55 cc/1,000 m^3.

High zooplankton volumes also occur in the area between lat. 2°S and 8°N at long. 150°W with peak abundance at lat. 1°S. Latitudinally, the average zooplankton volume is greater in the zone of convergence and the countercurrent than in waters of the South Equatorial Current (King and Hida 1957). This asymmetrical distribution is attributed to formation of oceanographic fronts in the transition zone between the Equator and the southern boundary of the countercurrent. Longitudinally, within the equatorial region, there is a gradient of increasing zooplankton abundance from long. 180° to 150°W.

In the western North Pacific near Marcus Island, plankton biomass at 0-500 m is 18 mg/m^3 but only 9 mg/m^3 to the southeast near Wake Island (Vinogradov 1968). At the northern periphery of the North Equatorial Current near the Marianas Trench, plankton biomass is also low varying from 8 to 11 mg/m^3 at 0-500 m. Vinogradov noted that the biomass also decreases sharply with depth; for example, at 2,000-4,000 m, the biomass is 0.13 mg/m^3 but at 4,000-8,000 m, it is only 0.012 mg/m^3, which is 140 times less than that found at corresponding depths of the Kurile-Kamchatka Trench.

In the Southern Hemisphere near the Phoenix Islands, the influence of the productive equatorial region is evident in greater plankton biomass. Here, it is relatively high, reaching 16 mg/m^3 at 0-500 m. Below 200 m, however, the biomass starts to decrease sharply, its distribution and magnitude at various depths being comparable to concentrations in the tropical waters of the Northern Hemisphere. Along the southern periphery of the South Equatorial Current, the plankton biomass is extremely low reaching only 5.5 mg/m^3 at 0-500 m. In deeper layers, it is slightly lower than concentrations in plankton-poor waters of the Northern Hemisphere.

Water to the south of the Tonga Trench is relatively poor in plankton. Here, the biomass reaches 13 mg/m^3 at 0-500 m but below that the concentration decreases sharply and the distribution is sparse, conditions which are typical of tropical waters of the Southern Hemisphere. In fact, the planktonic biomass at the 1,000-2,000 m layer is lower than that found at corresponding depths in such plankton-poor waters as the North Equatorial Current.

In the Solomon Sea, the water is very rich in plankton in the upper 500 m. Here, the plankton biomass reaches 38.0 mg/m^3 or nearly four times that found in waters of the North Equatorial Current. This difference in biomass persists to about 1,000 m, but at 1,000-2,000 m, the concentrations decrease somewhat so that the biomass is only 2.4 times greater than that of the North Equatorial Current at comparable depths.

Larvae of epipelagic and mesopelagic species are also encountered in the upper 300 m of the oceanic regions. Gorbunova (1971) observed that in the western tropical Pacific, there are, in addition to representatives of typical oceanic icthyofauna, large numbers of larval anchovy, *Stolephorus zollingeri*, and lancelet, *Amphioxides pelagicus*, which occur more commonly in coastal waters. Among mesopelagic species, larvae of *Gonostoma elongatum*, *Cyclothone alba*, *Symbolophorus evermanni*, and *Diaphus* sp. are most common.

In terms of biomass, myctophids constitute 86%-95% of the entire ichthyoplankton. Their absolute biomass, measured from collections made in the western Pacific, ranges from 2.15 to 31.22 mg/m^3 and averages 12.38 mg/m^3 (Parin, Gorbunova, and Chuvasov 1972). The concentration of myctophids in the surface layer at night is significantly greater than their average density in the 0-500 m layer.

5. BENTHOS

5.1 Coral reefs

The benthic fauna in waters around the Hawaiian Islands has been discussed by Doty et al. (1968). At Kealakekua Bay, on the island of Hawaii, the noteworthy features of the benthic fauna are the diversity of organisms, the densities of some species, and the occurrence of some of the more spectacular molluscs in relatively shallow water. There are 184 marine molluscs in Kealakekua Bay compared to 110 species in Kaneohe Bay on Oahu, which is much larger. A striking aspect of the urchin population is the rich abundance of slate pencil urchin, Heterocentrotus, which is also highly important along many areas of the Kona coast of Hawaii, but is generally uncommon in other areas of the Hawaiian Islands. Other urchins present in large numbers are Echinothrix, Echinometra, and Tripneustes.

Studies on bottom biocoenoses in the upper parts of island shelves in the western Pacific have shown that species diversity and biomass magnitude depend largely on the number of larvae of different species arriving there from regions with a diverse population (Golikov et al. 1973). The largest biomass, which averages 10 kg/m^2 and consists predominantly of lush growth of reef-forming corals, occurs along the coast of Papua New Guinea. Off New Caledonia, American Samoa, Western Samoa, and New Hebrides, the biomass of corals reaches 6-7 kg/m^2 whereas other animals account for 5%-10% and underwater plants account for 1%-7% of the total mean biomass of benthos. At Fiji and Nauru Islands, corals form a somewhat smaller biomass, reaching 2.7-3.0 kg/m^2, but other animals, which account for 10%-24%, and plants, which contribute 8%-14%, play more significant roles in the total benthic biomass. In the Ellice Islands (Funafuti Atoll), the average biomass of coral reaches 4.7 kg/m^2 whereas other animals and plants account for 3% and 30%, respectively, of the total benthic biomass. Golikov et al. (1973) found the lowest biomass of corals, averaging 1.2 kg/m^2, and the most significant role of plants in the biocoenoses, accounting for 38% of the total biomass, at Marakei and Butaritari Atolls in the Gilberts. A similar relationship between the biomass of corals and plants occurs at Lord Howe Island.

In most of the islands studied, life is less abundant at the 0-1.5 m depth. The biomass, population density, and related metabolic activity in the biocoenoses reach a maximum at depths of 2 to 8 m, where reef-forming corals are extensive. Depending heavily on the size and weight of dominant species, the biomass varies significantly with depth and by islands whereas population density depends primarily on fecundity, spawning, recruitment, and elimination. Maximum indexes of abundance and diversity of life are observed in areas where reef-forming corals are strongly developed. Golikov et al. (1973) concluded that a characteristic feature of the vast majority of tropical biocoenoses is the high biomass (more than 100 kg/m^2 in some areas) and a relatively low abundance of species population.

A survey of the macrofauna inhabiting lagoon deposits on Aitutaki in the Cook Islands yielded about 100 species. Among the groups were Polychaeta (27 species), Decapoda (20+ species), Gastropoda (31 species), and Pelecypoda (13 species). Of three main deposit zones--intertidal sand flat of the mainland, reef rim, and lagoon floor--the intertidal flat had fewer species than either of the other two zones (Gibbs 1975). Many of the sand-dwelling molluscs in the intertidal flat are highly regarded as food by the islanders (Banner 1952).

5.2 Other shallow-water areas (less than 200 m)

In waters just outside the coral reefs off Oahu, Strasburg, Jones, and Iversen (1968), who made 28 descents in a small research submarine to survey bottom fauna, reported that invertebrates occurring near rocky patches and ledges between 24 and 107 m include the starfishes, Culcita and Linckia, sea urchin, Chondreocidaris, beds of a hydrozoan or anthozoan which resembled Pennaria but with larger and heavier individuals, and spiny lobsters, Panulirus. On the sandy plains, they observed sponges and the protruding tubes of annelid, occasional cone shells near rocks, and brittlestars which appeared to be relatively abundant. Strasburg et al. estimated that at depths between 60 and 70 m, as much as two-thirds of the sea floor is covered by beds of pen shell, Atrina, packed together at a density of about 540/m^2. Beds of spatangid heart urchins, consisting of several thousand individuals spaced about 30 cm apart, occur at about 107 m.

At greater depths--between 107 and 116 m--the sloping plain drops off to steep cliffs, which plunge 60°-80° from the horizontal. Here, the coils of an antipatharian coelenterate, probably a species of Cirripathes, are rather common as are various starfish, sponges, and sea urchins down to about 192 m. At 137-183 m, beds of red coral, Stylaster and Corallium, are common.

5.3 Deep to very deepwater areas

Samples from an oligotrophic bottom under the North Pacific Central Water at a depth of 5,500 to 5,800 m showed a macrofaunal density averaging 115 individuals/m^2 (range 84 to 160/m^2), much the same as in northwest Atlantic gyre waters (Hessler and Jumars 1974). The bottom fauna, composed in the overwhelming majority of deposit feeders, was extremely diverse. Most species, however, appeared to be rare, occurring only once in the samples. Only three species showed any significant deviation from randomness in their distribution--one polychaete worm and tanaid crustaceans.

Among the macrofaunal taxa, polychaetes were by far the most abundant numerically constituting 55% of the total, followed by tanaid crustaceans at 18%. Bivalves and isopods were the next two most important groups, comprising 7% and 6%, respectively, of the macrofauna. All the other taxa represented less than 15%; individually, each taxon contributed not more than 2% to the fauna. Most of the major taxa are sparsely distributed and are either missing from most of the samples or represented by only one or two individuals. Only the polychaetes, tanaids, and bivalves are present in all samples. Isopods and scaphopods are present in more than half of the samples.

Some major taxa usually found in benthic samples are noticeably absent (Hessler and Jumars 1974). Among them are amphipods, cumaceans, and echinoids.

Meiofaunal taxa, which are only partially retained by the screen used in washing, are also present in reasonable abundance in the box-core samples. Despite the shortcomings of the samples, the meiofauna are numerically 1.5 to 3.9 times as abundant as the macrofauna. Always present are nematodes, by far the most abundant, copepods, and ostracods. Nematodes comprise 53% and copepods 13% of the total metazoan fauna. The combined meiofaunal taxa average 2.2 times (range 1.5-3.9) more numerically abundant than the macrofauna. Foraminifera appears to be an important portion of the community, but their abundance cannot be assessed accurately because of the inability to distinguish living and dead tests. Remains of probably xenophyophoridans also appear to be an important segment of the community.

The tests of living and dead foraminifera combined are extremely abundant, involving 135-1,808 individuals or chamber-fragments/core sample (average 759.8). One species is present in abundance of up to 160/m^2 (average 60). This quantity far exceeds the abundance of any metazoan species.

In the western Pacific, Moiseev (1969) showed that the benthic biomass in the oceanic regions is less than 0.05 g/m^2 and varies between 0.05 and 0.1 g/m^2 along a belt running from south of Japan to offshore Papua New Guinea. Along the eastern coasts of the Philippine and Papua New Guinea, the benthic biomass rises to about 10 g/m^2. The South China Sea region, according to Moiseev's figure, has a benthic biomass on the order of 0.05 to 0.1 g/m^2. By constrást, Moiseev pointed out that the benthic biomass in South Polar waters of the coastal regions of Antarctica is extremely high, varying between 450 and 500 g/m^2; however, the biomass composition is primarily sponge.

6. FISH STOCKS AND FISHERIES

6.1 The fisheries

Essentially, the fish fauna of the western central Pacific islands is similar to that found off Southeast Asia. There is, however, a considerable amount of difference in shelf and slope areas between these two regions. Whereas the western central Pacific islands have very little shelf and slope areas, Southeast Asian region includes nearly one-half of the shelf and continental slope areas to 2,000 m in the Pacific. The result is that there is little opportunity for trawl fishing off the western central Pacific islands. There are, however, high-seas fisheries resources such as those of tunas and billfishes (not discussed in this report). Furthermore, when the fishery resources of the myriad of islands are critically examined, the importance of subsistence fisheries is rather striking. For it is in this region that some of the most exotic small-scale fisheries in the world are found (Manar 1969).

A prominent feature, then, of the fisheries scene in the western central Pacific, is the existence of numerous islands whose inhabitants depend largely on artisanal fishing directed to fish and shellfish in coastal waters. Cole (1973) observed that there is no general agreement as to what constitutes artisanal fishery because conditions differ among countries. However defined, artisanal fishery is of a flexible and pragmatic nature. Artisanal fishermen may be found in coastal, estuary, lagoon, river, or lake fisheries, including aquaculture. With light capital investment, a low level of organization, and little specialized skill, artisanal fishermen fish mostly hand-operated gear from small boats. Productivity and incomes are usually low and catches are commonly sold fresh, salted, dried, or smoked for local consumption.

In the sections that follow, the fisheries of the western central Pacific islands are described.[1]

6.1.1 American Samoa

Much of the fishing being carried on in American Samoa is still of a subsistence type and confined to coastal waters, although in recent years a small commercial fishery has been developed. In many places, traditional fishing gears--spear, scoop net, cast net, gill net, trap, handline, and trolling line--are still employed. A small-scale fishery for "palolo," the wormlike sacs of eggs and sperm of a sea annelid, Eunice viridis, which are released by the adults, occurs in October-November (Van Pel 1961; Manar 1969; Otsu and Yoshida 1971).

Subsistence fishing, however, cannot meet the demand for fresh fish in the more populous areas. In fiscal year 1970, for example, American Samoa imported 900 MT of seafood including canned salmon, salted mackerel, and frozen bottom fish despite the availability of yellowfin tuna, Thunnus albacares, skipjack tuna, Katsuwonus pelamis, snappers, Lutjanidae, rockfishes, Serranidae, and other species in waters around the islands (Fishing News International 1972; Swerdloff 1972). Swerdloff has estimated that a domestic fleet could readily market fresh fish in excess of 450 MT annually.

In 1972, the first of the 7.3-m plywood Samoan dory, a modified version of the Pacific City (Oregon) dory, was launched (Fishing News International 1972; Office of Samoan

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[1] Throughout the remainder of this report, scientific names of fishes, crustaceans, molluscs, and echinoderms are used after the common name first appears and are repeated in some cases to avoid confusion. Where no scientific names are given, the author was unable to find them in the original report.

Information 1974). From December through March, about 75% of the fishing effort among the dories are expended in trolling for tuna whereas in the off-season for tuna, the dories spend about 75% of their time handlining for bottom fish at night (Naughton 1975[2]).

Major species caught by trolling are skipjack tuna, yellowfin tuna, mahimahi, Coryphaena hippurus, and kawakawa, Euthynnus affinis. Species of lesser importance include black marlin, Makaira indica, blue marlin, M. nigricans, dogtooth tuna, Gymnosarda unicolor, wahoo, Acanthocybium solandri, barracuda, Sphyraena forsteri, and rainbow runner, Elagatis bipinnulatus. Important species in the handline fishery are the green snapper, Lethrinus miniatus, red snapper, Lutjanus gibbus, jack crevally, Carangidae, dogtooth tuna, blue-line snapper, Lutjanus kasmira, groupers, Cephalopholis, Epinephelus, and Variola, barracuda, and bigeye scad, Trachurops crumenophthalmus.

6.1.2 Cook Islands

In the Cook Islands, a large proportion of the population is involved in fishing, which in most cases, is a semisubsistence activity in both inshore and offshore reef areas, lagoons, brackish-water ponds, creeks, and swamps (Van Pel 1961; FAO 1976a). There is no organized marketing system for fish; therefore, the fishermen sell their catches directly to the consumers.

Van Pel (1955) observed that in the reef area, which is overfished, islanders traditionally carry on some type of fishing--gathering shellfish or fishing for juveniles of giant clam, rock cod, Serranidae, and parrotfish using spear, scoop net, surround net, rock trap, and pole and line. In deeper waters, trolling line is used for surface schooling tunas, Spanish mackerel, Scomberomorus commerson, and particularly wahoo, and dip net and light (as an attractant) is used for flyingfish. Castor-oil fish, Ruvettus pretiosus, carangids, and barracuda are usually caught by handlines. At Aitutaki, northern Cook Islands, the main local fishing effort concentrates on netting in the lagoon for bonefish, Albula vulpes, goatfish, mullet, and bigeye scad, but there is also a seasonal fishery for yellowfin tuna from February to May (Hume 1976).

Although fishery development projects in the 1960's introduced powered outboard skiffs and modern fishing gears to the Cook Islanders (Powell 1962), there has been little progress since then in developing a commercial fishery (FAO 1976a). The growth and development of the industry is being impeded by shortage of suitable fishing boats and the lack of maintenance of those already in operation. Furthermore, use of illegal fishing methods such as dynamiting, poisoning, and netting with small-mesh nets have seriously depleted the stocks of fish in the lagoon.

6.1.3 Fiji Islands

Most fishing operations in Fiji are still little more than the traditional subsistence type and are carried on by about 2,000 fishermen. None of the 600 or more licensed, flat-bottomed fishing punts, about 5-8 m in length, is capable of sustained fishing in distant waters; therefore, the majority is unsuitable even for offshore fishing outside the reef (FAO 1972; Cole 1973; Aubray 1976). Using mainly handline and gill net within the lagoon, Fijian fishermen catch a wide variety of fish including mullet, mackerel scad, Decapterus pinnulatus, halfbeak, ponyfish, snappers, breams, Sparidae, bigeye scad, rabbitfish, Siganus sp., and milkfish, Chanos chanos. A number of important crustaceans including mud crabs, Thalamita sp., mangrove crab, Scylla sp., and mangrove lobster, Thallasina anomala, and several species of molluscs such as ark shell, Arca scapha, trochus shell, and mother-of-pearl are also harvested (Ministry of Agriculture, Fisheries and Forests 1976).

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[2] Naughton, J. J. 1975. Trip report, American Samoa, 18 July 1975. Western Pacific Program Office, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812, 12 p., unpublished.

6.1.4 French Polynesia

Both subsistence and commercial fishing are fairly active in French Polynesia, although frequently these two segments of the fisheries cannot be readily distinguished. Tahitian fishermen use dugout canoes, propelled by paddles, sails, and outboard motors in many types of fishing. Fishing usually takes place in the open coastal waters, lagoons, and over the reef.

In open-water fishing, Tahitian fishermen use small, fast boats called "bonitier" to fish for skipjack and yellowfin tunas (Brun and Klawe 1968). These "bonitiers," which can accommodate up to three men, frequently cruise over 185 km in a day's fishing (Hinds 1971; Doumenge 1973). No refrigeration is used; therefore, each vessel's crew guts the fish before returning to unload its catch. On a good day's fishing, one boat may land 200-300 fish.

In the lagoon, the fishing gears are the traditional types--trap, pot, handline, pole and line, cast net, beach seine, crab net, gill net, harpoon, and spear--and generally used only for small-scale fishing (Clutter 1972). Lagoon fishing with small nets accounts for about 4% of the fish sold. Fixed trap, which accounts for about 31% of the fish marketed in Papeete, is widely used in the Leeward, Tuamotus, and Gambier Islands. Large-net fishing, accounting for 7%-11% of the market catch, is confined to reef passages and along the coast for bigeye scad and mackerel scad. Other species that often reach the market in Papeete are skipjack and yellowfin tunas, which account for about 38% of the sales, spiny lobster, and mother-of-pearl shell. Bigeye scad and mackerel scad not immediately destined for sale are kept alive in impoundments constructed of either old fish nets or galvanized chicken wire fences and stakes.

6.1.5 Gilbert Islands

In the Gilbert Islands, fishing is a subsistence activity carried on by individual families (Hinds 1969). Nearly every family has its own canoe and most residents spend much of their time in their fishing crafts and are expert outrigger canoe handlers and fishermen. Also popular are outboard-powered 3.6-m fiber glass boats which in recent years have contributed to an increase in catch.

Trolling in canoes and small motorized boats mainly in coastal waters is the principal method for catching tuna and other pelagic species. Also used are the traditional pole-and-line method with mother-of-pearl lures, deep handline, and dip net. Troll catches include tuna, skipjack, billfish, jack crevally, and barracuda; deep handline fishing produces not only small amounts of tuna and billfish but also castor-oil fish and shark. Dip-net fishing by torchlight is used at night for flyingfish.

On the reef flats, the method of fishing varies widely from hand gathering of shellfish, octopus, spiny lobsters, crabs, and small fish, either day or night, to trapping with large stone traps (Hinds 1969). Other gear frequently used for reef fishing are pole and line, dip net, and spear.

In the lagoon area, underwater spearfishing, handlining, and net fishing are popular. Lagoon catches include parrotfish, mullet, grouper, and snapper. Sardines are occasionally caught with a cast net.

Fish catches are usually divided first among relatives and friends of the fishermen and the surplus is sold directly to other consumers. The few fishermen who engage in commercial fishing usually keep the retail markets supplied with fresh fish.

6.1.6 Guam

In Guam, as in American Samoa, there is a critical shortage of fresh fish. Ikehara, Kami, and Sakamoto (1972) estimated that the potential demand for fresh or frozen fish on

Guam is more than 900 MT, yet no commercial fishery exists in the island. The supply of fresh fish is usually provided by weekend recreational fishermen who sell part of their catches, which annually amount to less than 140 MT.

A narrow reef, which fringes the island except in the northern half of the east coast, is uncovered at low tide. Recreational fishing on the reef produces goatfish, parrotfish, snapper, mullet, surgeonfish, leatherjacket, wrasse, jack crevally, rockfish, garfish, tarpon, anchovy, and scad (Van Pel 1961). Squids and turtles are also present as are edible shellfish.

Gear most commonly in use on the reef include fixed fish trap or weir, cast net, set net, surround net, handline, and spear. Just off the fringing reef where only limited fishing takes place, handlining and netting, sometimes with light attraction, produce the bulk of the catch, mainly pelagic species.

6.1.7 Hawaiian Islands

In the Hawaiian Islands, where the marine fauna forms an offshoot of that great marine zoogeographic region centered on the East Indies, the species complex is not as diverse as in the western Pacific. Here, the shelf zone that characterizes most of the world's great fishing areas is narrow and poorly developed. The result is that only about 60 of the 682 species of fish, mostly found on the reefs and inshore area, are commercially exploited. Most are captured by a variety of gear including pole and line, longline, haul seine, bag net, pot, trap, gill net, anchor net, handline, and cast net. But the major thrust of the commercial fishery is in the open ocean beyond 200 m in depth, where pole-and-line sampans catch almost all the Hawaiian landings of skipjack tuna and longline boats harvest deep-swimming yellowfin tuna, bigeye tuna, Thunnus obesus, albacore, T. alalunga, striped marlin, Tetrapturus audax, blue marlin, black marlin, swordfish, Xiphias gladius, shortbill spearfish, Tetrapturus angustirostris, sailfish, Istiophorus platypterus, wahoo, and mahimahi.

The nearshore fisheries in Hawaiian waters are for a variety of demersal and bathypelagic species. In the handline fishery, for example, the major species include pink snapper, Pristipomoides microlepis, gray snapper, Aprion virescens, red snapper, Etelis carbunculus and E. marshi, amberjack, Seriola dumerilii, jack crevally, and other carangids, goatfish, Mulloidichthys samoensis, and sea bass, Epinephelus quernus. Bigeye scad, second only to tuna and billfish in total landings, is caught by three types of gear--bag net, which accounts for nearly two-thirds of the annual landings, handline, which lands about 20%, and gill net, which contributes about 13% (Kazama 1977). Also of importance in the Hawaiian fishery is the mackerel scad, which is widely distributed in the tropics and is found in small schools just outside the breakers and off coral reefs. The gears for capturing mackerel scad are the hoop net, which accounts for slightly more than half of the mackerel scad landings, and handline, which produces roughly 45% of the catch.

An important fishery that is often overlooked in the published statistics of the Hawaii Division of Fish and Game is that for anchovy, Stolephorus purpureus. Caught in shallow bays and harbors throughout the major Hawaiian group, the anchovy is used primarily as live bait in the pole-and-line fishery for skipjack tuna, although some are caught and processed for consumption.

Blessed with year-round ideal weather, Hawaii is also ideal for marine-oriented, recreational fishing. The Hawaii Division of Fish and Game estimated that about 169,000 residents or 20% of the population engage in marine recreational fishing, for a total of 6 million fishermen-days per year. Recreational fishermen pursue a wide variety of fish using a wide assortment of gear. But in terms of tonnage landed, trolling gear appears to be the most important. Major species landed by trolling are yellowfin tuna, mahimahi, wahoo, blue marlin, and striped marlin.

A few long-range commercial fishing vessels in the Hawaiian fleet operate in waters of the Northwestern Hawaiian Islands, which extends from Nihoa northwestward to Kure Island. Fishing primarily with handline, fish trap, and lobster pot not only around Nihoa and Necker but also as far north as French Frigate Shoals on occasion, these vessels catch mainly spiny lobster, sea bass, jack crevally, amberjack, pink snapper, gray snapper, and red snapper (Uchida 1977[3]).

Beyond the northernmost tip of the Hawaiian chain, a relatively new trawl fishery has developed for seamount resources. Until 1967, groundfish on the seamounts in the central North Pacific aroused very little interest primarily because most fishery scientists doubted the possibility that they could be exploited commercially. The discovery of commercial concentrations of pelagic armorhead, Pentaceros richardsoni, and alfonsin, Beryx splendens, on the Emperor Seamount Chain northwest of Midway Islands was made by a commercial trawler of the Soviet Union in November 1967 (Sakiura 1972). Almost immediately after the discovery, Soviet trawlers worked the banks and seamounts of this chain. Subsequent surveys by Soviet research vessels were concentrated on Kinmei Bank, Milwaukee Bank, and Hancock Seamount.

Fishing over seamount tops ranging from 100 to 400 m below the sea surface, the Soviet trawlers found schools of armorhead averaging 30 m thick and produced catches varying from 3 to 50 MT on 10- to 20-min hauls. Often, the catches reached 30 MT in a 10-min haul. Sakiura reported that the Soviet trawlers produced 133,400 MT (unconfirmed) of armorhead from these seamounts between December 1969 and July 1970.

In 1969, the Japanese started deepwater trawling over seamounts and banks in the central North Pacific, north of Midway. Working the grounds mainly for pelagic armorhead and alfonsin, the Japanese trawlers made fairly good catches. On one particular trip from mid-June to early August 1975, one Japanese trawler caught 280 MT of fish over the seamounts (U.S. NMFS 1975).

After the developmental years 1969-71, Japanese catches of armorhead began to stabilize at about 20,000-30,000 MT, but effort increased from about 500 h in 1972 to 2,700 h in 1976. The result was that catch per effort declined progressively from about 60 MT/h in 1972 to 10 MT/h in 1976 (Takahashi and Sasaki 1977). Up to 7% of the Japanese catches in 1969-76 was composed of alfonsin.

6.1.8 Nauru

The fishing industry in the Republic of Nauru has been described as quasi-commercial but on a relatively small scale (Clutter 1972). Power boats and locally built canoes are used in fishing, but because there is no direct distribution system, the fishermen sell their catches directly to the consumer. Under present conditions, this distribution system appears to be adequate to meet the demand.

The government is anxious to diversify sources of revenue and fisheries development appears to show good potentials. A feasibility study conducted recently evaluated the fishery development and processing of marine products in the Republic.

6.1.9 New Caledonia and dependencies

Fishing in New Caledonia is an important economic activity. Full- and part-time commercial and sport fishermen of several nationality including European, Indo-Chinese, Indonesian, Polynesian, and Melanesian engage in all forms of fishing activity (Van Pel 1961).

Commercial fishing crafts in New Caledonia include 9-12 m cutters with inboard engine, auxiliary sail and either a live well or refrigerated holds, small sailing boats for trochus gathering, and large numbers of miscellaneous fishing boats such as canoes, flat-bottomed punts, and cabin cruisers powered with outboard motors. In 1974, Sauvée (1974) reported that artisanal fishing was carried out in the lagoon by about 130 boats, 40 of which were considered operating on a truly commercial scale. Fishing is usually confined within the lagoon and on the reefs, although some deep-sea fishing takes place around the neighboring Loyalty Islands. A large proportion of the catch includes snapper, sweetlip, rockfish, mullet, Spanish mackerel, and surgeonfish. The gears most frequently used are handline, trolling line (some boats are equipped with outriggers for multiple trolling), surround net, gill net, seine, barrage net, cast net, spear, and bottom trap.

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[3] Uchida, R. N. 1977. A summary of environmental and fishing information of the Northwestern Hawaiian Islands. SWFC Admin. Rep. 4H, 60 p. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812, unpublished.

Studies have shown that New Caledonian waters are rich in tuna. Angot (1959) has shown that trolling gear was the most suitable for taking skipjack and yellowfin tunas. A commercial trolling fishery has been established in New Caledonia and the catch is sufficient to supply the demands of the Noumea market.

6.1.10 New Hebrides

New Hebrides has no large-scale commercial fishery. There is, however, a tuna-fishing industry established by American, British, French, and Japanese capital based at Palekula, which obtains tuna from Japanese longliners and exports them to various canneries.

Subsistence fishing accounts for most of the fresh fish and shellfish caught in waters around New Hebrides and any excess, usually only a small quantity, is sold in Port Vila and Luganville, two main centers of population. Canoes are in general use, but sailing and motor boats also contribute to the fish landings. The main types of gear are spear, handline, trolling line, cast net, small seine, bottom trap, and fixed trap (Van Pel 1961).

6.1.11 Niue

In Niue, which has no commercial fishery, fishing is essentially for subsistence and subsidiary to small-scale agricultural production (Clutter 1972). By custom, a Niue resident must be equally adept in agricultural practices and fishing.

Some 500 residents, mostly part-time fishermen, use single (about 320) and three-men (about 30) canoes, which are locally made, and primitive fishing methods to land about 10 MT of fish annually, supplying about one-sixth of the island's fish requirement. Among the gear in common use are handline, trolling line, and scoop net for flyingfish, which are usually captured at night. Fishing grounds for handlining are limited to areas on the eastward slope of the narrow, shelflike fringing reef.

6.1.12 Papua New Guinea and West Irian

Although the waters off the Papua New Guinea mainland and its 600 small islands support a rich and varied marine fauna, it was only in recent years that fishing became an important economic activity. From Papua New Guinea's waters, some 1,600 fish species, 5,000 molluscs, and about the same number of crustaceans have been identified but only a few--perhaps no more than 100--are utilized by the 100 or so licensed commercial fishermen and several thousand subsistence fishermen. Pownall (1972) estimated that the annual subsistence catch, about 20,000 MT, is insufficient to meet all needs, particularly in inland districts which depend heavily on frozen imports and processed fish. But efforts are underway to increase production through boat-building programs, introduction of motorized boats, and construction and demonstration of new nets, fishing techniques, and fish handling procedures.

Joint venture companies have had a tremendous impact in the rapid development of commercial fisheries, particularly for tuna and shrimp, in Papua New Guinea. Surveys conducted by commercial fishing boats and by the government's Research and Survey Branch revealed commercial concentrations of banana shrimp, Penaeus merguiensis, and skipjack tuna in waters of Papua New Guinea. Trawlers, licensed to operate under joint venture agreements, produced 349 MT of shrimp in 1970-71 (Pownall 1972). In the tuna pole-and-line fishery, one joint venture company operated in 1970 and produced 2,430 MT. By 1971, however, three ventures were operating and the catches in 1971-75 fluctuated between 13,100 and 42,050 MT.

Traditional fishing methods are still widespread in Papua New Guinea despite rapid development of fisheries for tuna, shrimp, spiny lobster, Panulirus ornatus, and barramundi, Lates calcarifer. Most of the inshore fishing is done from canoes but motor boats have increased in popularity (Hinds 1969). More than 3,000 outboard-powered canoes, dinghies, and other small crafts are actively engaged in fishing. The main types of gear include a variety of spears used in inshore waters, rivers, and lakes, an assortment of traps from the large Rabaul type to the single-handed cones for river and lake fishing, gill net which is popular for catching barramundi and reef fishes, surround net, scoop net, skimming net, pole and line, handline, and trolling line (Van Pel 1961; Pownall 1972).

Among the major species caught by subsistence fishing in the delta area are catfish, Tachysuridae, barramundi, jewfish, Sciaenidae, beach salmon, Leptobrama mulleri, threadfin salmon, Polydactylus sheridani and Eleutheronema tetradactylum, and mullet (about 10 species with Liza dussumieri commonest). Also caught are small numbers of bream, Acanthopagrus berda, mangrove jack, Lutjanus argentimaculatus, tripletail, Datmoides quadrifasciatus and Lobotes surinamensis, javelinfish, Pomadasys hasta, and leatherskin, Chorinemus lysan. Commercial exploitation of these species, with the exception of barramundi, is very limited (Fisheries Division and the National Investment and Development Authority (FDNIDA) 1976).

The development of the commercial fisheries revolved around four major resources--tuna and shrimp which are by far the most important followed by barramundi and spiny lobsters. The skipjack tuna fishery has been described by Kearney (1973, 1974) and Kanudi Fisheries Research Station (1977). For shrimps, surveys by Japanese research and commercial vessels have shown that the potential for a fishery, based on the availability and abundance of banana shrimps, is excellent. The shrimp fishery, which is the major fishery in the Gulf of Papua, had a modest beginning in 1955 but it evolved into a large commercial operation which in terms of effort and value of catch far outweighs other fishery development in the Gulf (FDNIDA 1976).

The spiny lobster, Panulirus ornatus, fishery is concentrated in three locations--around Daru in the western province, in the Gulf of Papua, and at Yule Island. Lobsters are fished year-round at Daru, from August to November at Kerema, and from January to April at Yule Island. At Yule, lobsters are captured alive, in Daru they are speared, and in the gulf, where the major fishery for lobster operates, they are caught by trawler (Wilson 1976). Barramundi, the fish in greatest demand in Papua New Guinea, constitute one of the most important resources of Daru and the western province. Their distribution is most dense in the Fly River basin area. The fish is caught in a seasonal coastal fishery which depends on migrating fish from the inland areas and also in an inland fishery.

Fishing in West Irian is mainly for subsistence and is quite active along the coast and neighboring island (Van Pel 1961). There is no commercial fishery in the island although some fishermen sell their catches around the main centers of population. Very little locally caught fish reach the interior.

Fishing is usually conducted from canoes propelled by paddle, sail or outboard motor, and from a few motorized boats. Spear, pole and line, handline, trolling line, bottom trap, reef trap, beach trap, reef net seine, gill net, dip net, and cast net are the main gears in use.

6.1.13 Solomon Islands

Fishing in the Solomon Islands is mainly a subsistence activity although fish in excess to a fisherman's immediate need are sold or bartered for other goods (Van Pel 1961).

Coastal villages fare better than those farther inland as they generally have sufficient fish to meet their nutritional needs. In other areas, for example, in the capital city of Honiara, the residents depend heavily on imported fish.

Most of the fishing crafts used are canoes propelled by paddles or sails. The Solomon islanders fish over the reefs and near-coastal waters using a wide variety of traditional gear including spear, harpoon, pole and line, handline, trolling line, lift net, scareline equipped with a bag net, surround net, gill net, turtle net, and dip net. Among the principle species caught are flyingfish, yellowfin tuna, kawakawa, Spanish mackerel, barracuda, jack crevally, skipjack tuna, and mahimahi.

Enactment of the 200-mile conservation and management zone vastly increases the developmental potential of the fishery resources of the Solomon Islands (James 1977b). The pole-and-line skipjack tuna fishery established in 1973 under a joint venture agreement between the Solomon Islands Government and Taiyo Fishing Company of Japan, has flourished and in 1976 was the single largest producer in the islands with exports values at $A7.5 million. Other species have also been targeted for further development. In fact, fisheries have developed in advance of the marketing infrastructure but with additional injection of capital, a more organized marketing structure should emerge. Among the species that are being exploited commercially are the spiny lobster, oyster, crab, and shrimp.

6.1.14 Tokelau Islands

In the Tokelau Islands, fishing and related activities are of the utmost importance (Van Pel 1961). Fishing is confined primarily on the reef and inside the lagoon the year-round and outside the lagoon in favorable weather and is conducted mainly from outrigger canoes which are built of planks and propelled by paddle or sail. While the catch usually includes a wide assortment of reef species, ocean fishing provides species such as tuna, Spanish mackerel, bonito, jack crevally, shark, and barracuda. Flyingfish is captured at night with torchlight and dip nets. The outer reef is also fished for bigeye scad practically all year.

6.1.15 Tonga Islands

Tonga has no organized fishing industry in a strictly commercial sense. The industry lacks professional fishermen and is at a very early stage of development, based mainly on the inshore and nearshore fish resources (Wilkinson 1974). There are between 1,300 and 1,400 residents engaged in fisheries in the southern and central islands and an additional 300 in the northern islands (FAO 1975a). Among the 500 small crafts in use are outrigger canoes, skiffs with outboard motors, launches with inboard engines, and sailing boats.

The fishing gear used are the traditional types including spear, gill net, trammel net, beach seine, cast net, coconut frond net, turtle net, handline, and pole and line (Williams 1969). The main fisheries are based on reef and inshore handlining, commonly conducted at night with light attraction, surface trolling, and trapping (Lorimer and Maclean 1974; FAO 1975a).

Longline fishing within Tongan waters began in 1970 and continues to show relatively good progress. In 1976, the longliner "Ekiaki" fished 107 days by the end of October and produced 117 MT of deep-swimming tunas and billfishes (Wilkinson 1977a). A second longliner, donated to Tonga by the Japanese Government, is slated for service with an all-Tongan crew.

The inshore lagoon and near reef catches consist of a wide assortment of tropical species including jack crevally, flyingfish, Spanish mackerel, barracuda, parrotfish, snapper, goatfish, and milkfish. Most fish marketed are small or juveniles of large species, usually 15 to 25 cm in length. Among the main species marketed throughout the year are juvenile emperor, Lethrinus variegatus, rabbitfish, Siganus oramin, and bigeye scad. Unicornfish, Naso unicornis, blue-line snapper, triggerfish, tuskfish and other labrids, and longtom, are also common (Lorimer and Maclean 1974). Porcupinefish and stonefish are frequently sold for consumption. Mullet, Mugil cephalus, occur in abundance in August-November and dominate landings at this time.

Among various other marine animals harvested for consumption are holothurians (bêche-de-mer) of which only the intestines are marketed, large, short-spined sea urchins, which are very popular, and octopus, which are either sold fresh or dried and smoked.

6.1.16 Trust Territory of the Pacific Islands

In the Trust Territory, as in most other Pacific islands, subsistence fishing is an important daily activity. Most fishing takes place on the reefs and in the lagoons. Canoes with and without outriggers and propelled with paddles, sails or outboard motors, are still quite commonly used. There is also an increasing number of modern motorized vessels in use. The main fishing gears include handline, trolling line, pole and line, beach seine, surround net, gill net, dip net, cast net, scareline, spear, fixed traps of rocks or wire, and bottom trap. Fish caught and landed in excess of an island's need, for example at Palau and Ponape, are exported to other islands of the Trust Territory and Guam (Van Pel 1961).

The inshore waters in Micronesia are presently not suitable for major commercial exploitation because of the limited productivity of the coral reefs and the "territorial" characteristics of many of its inhabitants. Furthermore, past practices of intensive fishing with gill nets and seines and the use of mechanized crafts have partly contributed to severe depletion of the inshore resources (Rechebei 1977).

6.1.17 Tuvalu

Tuvalu, formerly known as the Ellice Islands and which were separated from the British colony of Gilbert and Ellice Islands and formed into a new colony on 1 October 1975, has a vital stake in developing its fish resources, because there is very limited alternate resources that could be developed to boost the country's economy. In a pre-European economy, Ellice islanders were subsistence fishermen, catching indigenous marine fishes and shellfishes with traditional fishing gears in outrigger canoes (South Pacific Commission 1977c). Today, fishing is still domestic in character and very little commercial exploitation occurs despite a continuing strong demand for fresh fish (see 6.1.5 Gilbert Islands for information on fishing in Tuvalu).

6.1.18 Wallis and Futuna Islands

From reports of the South Pacific Commission (1977b), it is evident that a serious decline in primitive subsistence fishing has occurred in the Wallis and Futuna Islands. By 1970, only a few traditional canoes remained on the islands. Clutter (1972) reported that these canoes are heavy and difficult to maneuver; therefore, the fishermen never venture into the open ocean beyond the encircling reef, where scombrids such as dogtooth tuna, Gymnosarda nuda, Spanish mackerel, Scomberomorus commerson, and wahoo, Acanthocybium solandri, are present. Instead, the residents concentrate continuous and undesirable fishing pressure on the lagoon stock using handlines and nets. The result is that there has been a serious decline in the lagoon stock and supplies of fresh fish are insufficient to meet the local demand, which is satisfied by imported canned fish and beef.

6.1.19 Western Samoa

In Western Samoa, fishing is basically a subsistence activity, although some commercial fishing occurs; there is no organized fish market through which the fish are sold. Fishing is concentrated primarily on the fringing reefs and lagoons. The Western Samoan fishermen catch any edible organisms, irrespective of size, including fish, shells, crustaceans, turtles, bêche-de-mer, squids, octopus, and sea urchins as well as large quantities of "palolo" when in season. In use are 1,500 canoes and 50 catamarans, all powered with outboard motors (Van Pel 1961; FAO 1975b).

To capture their prey, the fishermen use fixed fish traps, gill net, beach seine, stake net, eel trap, spear, pole and line, trolling line, handline, and cast net. There are about 7,000 part-time fishermen using mainly spear and net to harvest organisms from the reef area. The result is that there is considerable fishing pressure exerted and the reef and lagoon fauna are undoubtedly overfished. Fortunately, schools of bigeye scad enter the lagoons occasionally, thus relieving some of the pressure on the reef stock.

Trolling for tuna is another of the principal methods of fishing (Gulbrandsen 1977). Using motorized double-hulled canoes and fishing outside the reef, about 400 Western Samoan fishermen find trolling one of the most economical ways to fish because of the low initial investment in gear, simplicity of the technique, and the recreational value involved. Despite the seasonally good catches made by these trollers, there are periods when the availability of tuna is either very low or tuna are entirely absent from Western Samoan waters. Therefore, to insure profitability of these trollers, bottom handline fishing along the outer reef was begun in 1975.

Good bottom fishing grounds are usually located at the drop-off of the outer reef at depths between 100 and 150 m. Because currents around the islands are generally swift, the boats anchor on the grounds. The major species caught by handlining in Western Samoan waters include shark, sharptooth snapper, Pristipomoides typus, rosy job fish, Aprion microlepus, Malabar red snapper, Lutjanus malabaricus, longface emperor, Lethrinidae, castor-oil fish, red snapper, L. bohar, grouper, Serranidae, green job fish, A. virescens, snake mackerel, Promethichthys prometheus, and small-toothed job fish, Aphareus furcatus.

6.2 Statistics

Catch statistics from western central Pacific islands are summarized for 1965-75 in Tables 3 and 4, by islands and species groups, respectively. Although several island governments have implemented fish catch data collection systems in recent years, none of the statistics are entirely satisfactory.

The data collection system in American Samoa was started in 1971 and has shown steady improvement. Three systems were set up initially--one for the Samoa-based longline fishery for albacore, another for the Samoan-dory commercial operation, and a third for the subsistence fishery among the many outlying villages. Of a potential sample size of 1,550 vessel trips among the longliners in 1971-73, data on albacore lengths were obtained from 82% and on catch and effort from 76% of them. For the Samoan-dory fleet, standardized catch and effort reports were collected from about half of the trips recorded. Attempts to collect subsistence fishing data, however, proved to be fruitless, because the catches reported by many of the villages were considered unreliable (Sesepasara 1973; Office of Marine Resources 1976).

In French Polynesia, Tahitian yellowfin and skipjack tuna catches actually represent only about a third to a half of the true tuna production. There are two important sources of error: First, because all the yellowfin and skipjack tunas are gutted at sea, the landings at Papeete Municipal Market represent weights of eviscerated fish (Brun and Klawe 1968) and second, many fishermen bypass the Papeete Market and dispose of their catches directly to local fish dealers or through roadside and door-to-door sales (Doumenge 1973).

The most extensive statistics are for the commercial fisheries of the Hawaiian Islands, but these too are deficient in certain categories. For example, they exclude (1) catches made by many of the recreational fishermen who do not obtain commercial fishing licenses and, therefore, are not subject to reporting their catches, and (2) detailed data on the amount of fishing effort expended except in the well-developed skipjack tuna pole-and-line fishery.

Table 5 lists several fish groups and the annual catches of the important species within them for 1961-75 for the Hawaiian Islands. Landings by types of gear used and number of licensed fishermen and boats, by islands, are given in Table 6. Table 7 gives the catch, effort, and catch per effort in the Japanese trawl fishery for armorhead and alfonsin on the central North Pacific seamounts.

At present, it is difficult to estimate the production of fish in Papua New Guinea. In the case of subsistence fishing, the trade and sale of fish is very widespread. The result is that statistics are difficult to obtain, although some data from fisheries market surveys, fishing groups, fishing surveys, and cooperatives are available; however, the extent to which data from these sources reflect the total local trade in fish, and relationship of commercial production to subsistence fishing remains to be evaluated. Licensed fishermen are required to furnish the best data available on effort and catch; the data collected, however, are unsatisfactory and incomplete (Conroy 1972).

Catch data from the Trust Territory of the Pacific Islands have been judged to be gross underestimates because they represent only fish sold through the major fishing cooperatives. Catches sold directly to consumers are not recorded (Rechebei 1977).

6.3 Stock assessment

With the exception of the tuna resources, very little work on stock assessment, by species, has been carried out in this area, primarily because the commercial fishery in many of the island groups are still in its infancy. The one exception is in the Hawaiian Islands where limited assessment studies on some species have been completed and others are in progress.

Table 3.--Nominal catches of fish, crustaceans, and molluscs in the western central Pacific islands (in metric tons) (FAO 1970, 1975c, 1976b).

	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
American Samoa	--	--	--	--	--	00	--	--	100	82	--
Christmas Island	--	--	--	--	--	--	00	00	00	0	0
Cook Islands	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000
Fiji Islands	--	--	--	--	--	4,100	4,200	4,800	5,100	4,261	4,868
French Polynesia	1,900	2,100	2,000	2,100	2,300	2,300	2,200	2,400	2,600	2,386	2,169
Gilbert Islands	--	--	--	--	--	200	500	500	500	750	750
Guam	100	100	200	100	200	200	100	100	100	92	122
Hawaiian Islands[1]	9,089	6,086	5,552	6,096	4,577	5,310	8,020	6,911	6,759	5,372	4,624
New Caledonia	900	800	500	500	500	500	500	500	800	868	900
New Hebrides	3,400	6,200	5,400	7,900	8,000	8,000	8,000	8,000	8,000	8,000	8,000
Papua New Guinea	11,000	11,000	14,000	14,000	14,000	18,700	33,300	29,900	48,500	52,708	42,748
Solomon Islands	--	--	--	--	--	1,000	5,700	8,800	7,300	11,585	8,711
Tonga Islands	--	--	--	--	--	--	500	500	600	726	901
Trust Territory of the Pacific Islands	700	800	1,000	1,000	1,000	1,000	1,000	400	6,300	3,360	3,360
Tuvalu	--	--	--	--	--	--	00	00	00	0	0
Western Samoa	900	900	900	900	900	900	900	900	900	900	1,000

00 = More than zero but less than 50 MT.

0 = More than zero but less than 0.5 MT.

[1] Data are from Hawaii Division of Fish and Game, commercial fish catch, by species, 1965-75, mimeo.

Table 4.--Nominal catches of marine fishes in the western central Pacific islands (in metric tons) (FAO 1970, 1975c, 1976b).

	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
Herrings, sardines, anchovies, etc.											
Gilbert Islands	--	--	--	--	--	--	--	--	--	105	105
Hawaiian Islands	211	185	187	209	177	196	236	229	245	242	214
Papua New Guinea	--	--	--	--	--	--	--	--	--	1,000	750
Jacks, mullets, etc.											
Gilbert Islands	--	--	--	--	--	--	--	--	--	95	95
Hawaiian Islands[1]	422	520	605	672	584	639	609	612	537	493	505
Mackerels, snoeks, cutlassfishes, etc.											
French Polynesia	200	200	200	200	200	200	--	--	--	--	--
New Hebrides	00	300	400	900	100	100	1,000	1,000	1,000	1,000	1,000
Milkfish											
Gilbert Islands	--	--	--	--	--	--	--	--	--	50	50
Hawaiian Islands[1]	9	11	6	15	14	12	8	4	5	7	4
Redfishes, basses, congers, etc.											
Gilbert Islands	--	--	--	--	--	--	--	--	--	245	245
Hawaiian Islands[1]	207	224	220	188	209	179	196	211	241	221	269
Marine fishes (N.E.I.)											
American Samoa	--	--	--	--	--	00	--	--	100	33	--
Christmas Island	--	--	--	--	--	--	00	00	00	0	0
Cook Islands	400	400	400	400	400	400	400	400	400	400	400
Fiji Islands	--	--	--	--	--	4,100	4,200	4,300	4,300	3,700	4,240
French Polynesia	2,900	3,200	3,200	3,200	3,200	1,400	1,500	1,600	1,900	1,673	1,566
Gilbert Islands	--	--	--	--	--	200	200	200	300	300	--
Guam	100	100	200	100	200	100	100	100	100	92	122
Hawaiian Islands[1]	8,199	5,094	4,485	4,958	3,487	4,172	6,837	5,709	5,577	4,291	3,520
New Caledonia	500	400	400	400	400	400	400	400	600	600	650
New Hebrides	00	200	200	200	200	200	200	200	200	200	200
Papua New Guinea	9,800	9,800	11,700	11,700	11,700	16,000	16,000	16,000	19,000	5,000	15,000
Solomon Islands	--	--	--	--	1,000	1,000	1,000	1,000	1,000	1,000	1,000
Tonga Islands	--	--	--	--	--	--	500	500	600	726	901
Trust Territory of the Pacific Islands	700	800	1,000	1,000	1,000	00	00	00	100	145	145
Tuvalu	--	--	--	--	--	--	00	00	00	0	0
Western Samoa	900	900	900	900	900	900	900	900	900	900	1,000

00 = More than zero but less than 50 MT.

0 = More than zero but less than 0.5 MT.

N.E.I. = Not elsewhere included.

[1] Data are from Hawaii Division of Fish and Game, commercial fish catch, by species, 1965-75, mimeo.

Table 5.--Nominal catches of fishes, crustaceans, and molluscs in Hawaii.[1]

	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
Tunas, bonitos, billfishes															
Skipjack tuna, *Katsuwonus pelamis*	4,942	4,271	3,674	4,093	7,329	4,257	3,647	4,227	2,705	3,334	6,051	4,952	4,875	3,373	2,293
Yellowfin tuna, *Thunnus albacares*	208	180	175	227	226	228	228	188	192	320	389	375	349	523	781
Bigeye tuna, *T. obesus*	471	554	430	380	351	346	294	256	322	216	214	229	185	187	157
Striped marlin, *Tetrapturus audax*	103	125	152	228	175	144	181	188	144	156	87	78	64	89	106
Pacific blue marlin, *Makaira nigricans*	7	83	86	79	78	67	66	48	68	101	50	25	38	56	48
Wahoo, *Acanthocybium solandri*	12	11	14	15	14	10	18	13	16	20	18	24	34	33	53
Other tunas	7	14	34	20	10	21	34	24	30	17	24	25	29	25	73
Other billfishes	136	24	13	19	15	21	17	13	10	7	4	1	2	1	7
Redfishes, basses, congers															
Snappers, Lutjanidae	96	125	134	133	107	118	115	109	101	74	95	119	127	123	164
Goatfishes, Mullidae	61	48	58	57	49	45	36	30	37	36	34	36	41	33	33
Sea bass, Serranidae	9	10	15	11	10	15	11	10	10	18	22	17	23	18	27
Various reef species	45	40	49	50	41	46	58	39	61	51	45	39	50	47	45
Jacks, mullets, sauries															
Mahimahi, *Coryphaena hippurus*	53	49	58	39	41	39	33	33	26	34	52	79	52	50	53
Amberjack, *Seriola dumerilii*	35	39	48	43	34	45	31	39	33	32	38	26	30	15	14
Bigeye scad, *Trachurops crumenophthalmus*	130	99	68	73	204	283	387	429	362	445	371	394	325	284	232
Mackerel scad, *Decapterus pinnulatus*	95	174	182	133	86	100	96	111	98	79	104	78	94	98	146
Other jacks, mullets, barracuda	76	66	73	79	57	53	58	60	65	49	44	35	36	46	60
Herrings, sardines, anchovy															
Bonefishes, ladyfishes, Albulidae, Elopidae	14	8	14	14	13	13	13	16	13	13	7	17	18	18	11
Anchovy, *Stolephorus purpureus*	202	186	178	167	198	172	173	193	164	183	229	212	227	223	203
Marine crabs															
Frog crab, *Ranina serrata*	8	14	8	4	6	4	9	17	16	18	23	33	21	17	8
White crab, *Portunus sanguinolentus*	1	1	1	3	4	3	2	1	10	18	19	17	13	26	16
Other crabs	4	3	2	4	3	5	3	3	2	3	3	2	2	1	1
Lobsters															
Spiny lobsters, *Panulirus penicillatus* and *P. marginatus*	6	4	5	4	4	2	2	2	4	2	3	2	2	2	-
Molluscs															
Octopus, *Polypus marmoratus*	2	2	3	3	3	3	4	3	2	3	4	5	6	5	4
Squid, *Sepioteuthis arctipinnis*	4	5	2	4	1	3	1	2	1	3	6	1	5	2	2
Limpet, *Cellana* sp.	5	5	9	9	6	12	11	12	10	10	6	8	9	8	8

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[1] Data are from Hawaii Division of Fish and Game, commercial fish catch, by species, 1961-75, mimeo.

Table 6.--Fish and shellfish catches, by type of gear, number of licensed commercial fishermen, and number of commercial fishing boats, Hawaiian Islands (Power 1963; Power and Lyles 1964; Lyles 1965, 1966, 1967, 1968, 1969; U.S. National Marine Fisheries Service, 1971, 1975, 1976; Wheeland 1972a, 1972b, 1975; Thompson 1974; Pileggi 1976; and files of the Western Pacific Program Office, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812).

	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
Catch by gear:															
Lines - Hand and pole and line	5,133	4,490	3,912	4,576	7,740	4,698	4,097	4,682	3,127	3,674	6,573	5,481	5,401	3,962	3,069
Longline	1,100	1,157	1,096	854	774	751	709	612	642	698	522	478	353	377	339
Troll	20	25	32	37	40	44	55	31	60	79	54	61	110	224	424
Nets - Haul seines	238	203	194	191	218	185	213	213	207	202	233	215	246	228	208
Bag nets	100	66	46	57	155	219	314	336	260	326	244	268	201	119	84
Gill nets, anchored	28	15	26	27	29	40	44	48	48	66	62	82	96	139	115
Lift nets	46	104	94	70	45	54	52	66	55	53	72	64	68	64	54
Cast nets	--	--	1	2	1	2	3	2	4	3	3	2	3	3	2
Unclassified	7	14	22	18	23	26	15	7	6	4	5	5	15	3	5
Pots and traps	57	50	50	54	41	37	31	31	35	51	52	46	37	50	34
Spears	--	--	2	2	2	3	3	2	2	2	3	3	4	4	3
Hand	--	--	4	7	1	2	2	2	2	2	1	2	4	4	2
Other marine gear	4	4	<1	1	3	3	3	1	35	27	50	52	48	22	32
Pond gear	32	24	20	23	10	10	5	5	9	9	7	6	7	11	8
Licensed commercial fishermen															
Oahu	345	371	396	360	372	412	391	596	763	781	812	912	1,083	1,044	1,115
Hawaii	114	194	174	162	156	128	119	172	220	317	380	415	565	556	671
Maui	80	123	129	105	109	109	90	149	233	207	197	204	241	192	228
Kauai	27	52	52	56	52	42	55	72	81	84	96	101	139	138	145
Molokai	16	53	47	42	43	39	33	27	26	37	36	55	47	47	23
Lanai	7	24	22	18	12	14	11	16	15	10	18	10	16	15	15
Commercial fishing boats															
Oahu	149	203	212	203	188	196	201	286	350	360	395	410	507	410	515
Hawaii	53	79	101	99	89	62	57	97	155	204	290	317	425	397	475
Maui	36	50	56	61	59	71	64	78	108	112	116	97	127	116	141
Kauai	22	47	46	48	43	36	39	57	57	69	79	73	101	108	119
Molokai	13	21	17	12	18	16	15	13	10	17	14	25	29	25	19
Lanai	7	14	7	8	7	7	7	12	12	6	9	6	9	10	9

Table 7.--Catch, effort, and catch per effort of armorhead and alfonsin caught by Japanese trawlers over the central North Pacific seamounts in 1969-76 (Takahashi and Sasaki 1977).

Year	Catch		Effort	Catch per effort	
	Armorhead (MT)	Alfonsin (MT)	(h)	Armorhead (MT)	Alfonsin (MT)
1969	8,280	27	157	20.892	0.172
1970	30,047	618	2,807	10.704	0.220
1971	5,891	68	1,304	4.525	0.052
1972	29,880	59	496	60.242	0.120
1973	25,047	34	740	33.847	0.046
1974	34,538	0	1,583	21.818	0.000
1975	18,952	0	1,377	13.763	0.000
1976	25,795	1,726	2,667	9.672	0.647

6.3.1 Anchovy, *Stolephorus purpureus* and *S. heterolobus*

The anchovy, *S. purpureus*, is a small (40-60 mm), fragile fish that school over sand and mud bottoms in scattered harbors and bays throughout the Hawaiian Islands. It possesses most of the qualities of good baitfish; therefore, it is the preferred bait in the Hawaiian skipjack tuna fishery (Uchida in press).

Regarded as one of the more important fish resources in the Hawaiian Islands because of its direct association with the skipjack tuna fishing industry, this anchovy, known locally as nehu, has been widely studied by several investigators (Hiatt and Tester 1950; Welsh 1950; Hiatt 1951; Tester 1951, 1955; Yamashita 1951; Tester and Hiatt 1952; Bachman 1963, Uchida in press; Wetherall in press). In determining the relationship between average catch per day of baiting and the number of days of baiting for three different baiting grounds in Hawaiian waters, Bachman (1963) determined that in 1948-60, there was no evidence that fishing had diminished the stock in Kaneohe Bay, Pearl Harbor, and Maalaea Bay. The Schaefer (1954) method for maximum sustained yield and catchability produced results for the stock fished at Pearl Harbor only. In the day-bait fishery here, the maximum sustained yield was calculated to be 18,620 buckets (100 MT), obtained at a fishing intensity of 691.5 boat days; catchability coefficient was -0.0022, a negative, meaningless value.

More recently, Wetherall (in press) examined nehu catch and nominal effort statistics from the Kaneohe Bay day-bait fishery to explore two sources of variation in baiting success: (1) nehu stock abundance and (2) abiotic environmental variables. The results showed that availability, catchability, or both, are reduced in January-April when rainfall is high and streamflow heavy, and enhanced in June-October when streamflows drop. Baiting success, however, was unrelated to nominal baiting effort.

For the skipjack tuna fishery in Palau, Muller (in press) determined a von Bertalanffy growth equation for *S. heterolobus* from length frequencies of fish collected from the commercial fishing fleet from December 1971 to July 1973:

$$L_t = 91\ (1-\exp(-0.0058(t + 3.4)))$$

where L_t = standard length in millimeters and

t = days

Total mortality for the 19-mo period was 6.0 yr^{-1} and average fishing mortality reached 3.0 yr^{-1}. Using the logistic models of Schaefer (1954) and Fox (1970), Muller obtained a maximum sustainable yield of about 80,000 buckets (160 MT) with an effort of under 2,000 boat nights. The dynamic pool model of Beverton and Holt (1957) gave the maximum yield per recruit at a fishing mortality of 5.0 yr^{-1}; however, at 3.6 yr^{-1}, or 2,000 boat nights, the yield per recruit was within 1.8% of the maximum. Muller concluded that the bait fishery in Palau is operating at the optimum level.

6.3.2 Bigeye scad, Trachurops crumenophthalmus

Excluding tunas and billfishes, the most heavily exploited major fish stocks are those of bigeye scad. Most of the fishing occurs in the Hawaiian Islands and French Polynesia. In Hawaii, the catches show wide annual fluctuations varying from around 70 to 444 MT in 1948-75. Kawamoto (1973) observed that present management regulations--the restriction of mesh size to not less than 3.8 cm and prohibition on netting fish of less than 21.6 cm in July-October--are presently effective because catches appear to be stabilized at a relatively high level of 360 MT annually.

6.3.3 Pelagic armorhead, Pentaceros richardsoni

There appears to be some indication that the pelagic armorhead stock has started to decline. Three Japanese trawlers fishing for this species off Midway atoll reported an average catch of 30 MT/day, considerably less than the break-even level of 40 MT/day (U.S. National Marine Fisheries Service 1976). These Japanese trawlers reported that armorhead landings in this area have declined sharply after a Soviet trawling fleet worked the same grounds for armorhead.

6.4 Other estimates of potential: Fishing surveys and exploratory fishing

6.4.1 American Samoa

Surveys in American Samoa in recent years have been concentrated on evaluating the potentials of bottom fishing, trolling, and pole-and-line fishing with live bait. On 19 research cruises of the research vessel "Alofaga," bottom fishing and trolling were combined and the total catch during that trial period amounted to 1,608 kg or about 85 kg/trip (South Pacific Commission 1977a). Fifty pole-and-line fishing trips with live bait yielded 14.2 MT or an average of 284 kg/trip.

Another of the important projects designed to boost American Samoa's economy is the evaluation of sport fishing development. During a 5-yr period in which 135 sport fishing surveys were conducted, 1,098 fish, weighing 5,800 kg or an average of 43 kg/trip, were caught. On an average trip of 5.8 h, therefore, the potential sport fishing catch reached 8.1 fish/trip. Among the species taken by the trolling gear were Pacific blue marlin, mahimahi, and skipjack tuna.

6.4.2 Cook Islands

In 1975, an outer-reef fishery project, which was started to survey the demersal and pelagic resources at Aitutaki, demonstrated that trolling for pelagic fishes, except wahoo, and bottom fishing during daylight would be economically unfeasible (Hume 1976). At night, however, handline catches were relatively good so that a reasonable return could be expected. The average catches from bottom fishing reached 71.4 kg/night-trip and 29.0 kg/day-trip, whereas the catch rates by trolling was only 25.9 kg/trip.

6.4.3 Fiji Islands

The potential for increasing fish yield in Fiji lies in harvesting the resources over the continental shelf. Aubray (1976) has estimated that perhaps 70% of the average potential yield of 15,000 MT, based on a minimum production of 15 kg/ha, would consist of demersal fish whereas the remaining 30% would constitute tuna and other pelagic species.

One of the pelagic species that has a tremendous potential for development is Spanish mackerel, *Scomberomorus commerson*. In 1975 and 1976, an estimated 20 and 26 MT, respectively, of this species were marketed in Fiji. Results of exploratory surveys in nearshore pelagic waters have shown that whereas the bulk of the Spanish mackerel taken prior to 1976 was by handlining, surface trolling is less labor-intensive and, therefore, more appropriate for catching this species (Brown 1977).

6.4.4 Hawaiian Islands

The Hawaii Division of Fish and Game, actively pursuing programs designed to develop new commercial fisheries, introduced marine species which have potentials for development as commercially exploitable resources in Hawaiian waters between 1955 and 1961. Of six species of groupers and five species of snappers introduced (Table 8), at least three species--*Cephalopholis argus*, *Lutjanus vaigiensis*, and *L. kasmira*--became fairly well established in Hawaiian waters (Hawaii DLNR (Department of Land and Natural Resources) 1969). Fishing for these species was opened to the public in October 1966 and at present *L. vaigiensis* and *L. kasmira* are caught by both sport and commercial fishermen.

Table 8.--Summary of the status of groupers and snappers introduced to Hawaiian waters (Hawaii DLNR 1967).

	Total number released	Year												
		1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967[1]
Groupers														
Roi, *Cephalopholis argus*	2,385		R	X	X		X	R-X	X	X	X	X	X	X
Tarao,[2] *Epinephelus merra* and *E. hexagonatus*	2,612		R					R-X	X	X	X	X	X	X
Rero, *C. urodelus*	1,811				R-X	X	X	R-X		X	X	X	X	X
Matapuu, *E. fasciatus*	51				R-X	X	X	X						
Pukokoo, *E. spiniger*	22				R-X				?					
Snappers														
Toau, *Lutjanus vaigiensis*	2,232	R	R		R-X		X	R-X	X	X	X	X	X	X
Taape, *L. kasmira*	3,168	R			R-X	X	X	R-X	X	X	X	X	X	
Tuhara, *L. gibbus*	177				R			R-X	X				?	?
Aaravi, *Lethrinus* sp.	32		R		R			R						
Mexican snapper, *Lutjanus guttatus*	3,439						R-X	X		X				

[1] To 30 June 1967.

[2] *Epinephelus merra* and *E. hexagonatus* grouped together as "Tarao" due to similarity in appearance.

R - Year of release.

X - Species caught or sighted during the year.

? - Unconfirmed report of sighting.

Another project designed to increase fish populations is the creation of artificial reefs and the results appear to be extremely encouraging (Hawaii DLNR 1966). Creation of these artificial shoals with old auto bodies and damaged concrete pipes has significantly increased fish populations. The fish counts, however, show wide variations. At Waianae, Oahu, for example, estimates of the standing crop varied from 550 kg/ha to 1,444 kg/ha. Kanayama and Onizuka (1973) attributed the wide variation in fish densities to schools of surgeonfish, Naso unicornis and N. hexacanthus, gray snapper, amberjack, and mackerel scad, which wander freely in and out of the shoal area. Furthermore, artificial shoals have attracted commercially valuable species such as squirrelfish, Myripristis berndti, goatfish, Mulloidichthys auriflamma and M. samoensis, jack crevally, Carangoides ferdau, Japanese barracuda, Sphyraena helleri, and surgeonfish, Acanthurus olivaceus and A. dussumieri (Hawaii DLNR 1967).

In general, for three areas in which artificial shoals were created, fish densities have increased tremendously. At the Waianae, Oahu auto-body reef, the pre-reef density in 1962 reached 115 kg/ha; the post-reef values averaged 1,424 kg/ha or more than 12 times the pre-reef density (Kanayama and Onizuka 1973). The post-reef average reached 556 kg/ha where concrete pipes were used. At Maunalua Bay, Oahu, where the pre-reef density was only 41 kg/ha in 1960, the post-reef density averaged 938 kg/ha. The densities at Keawakapu, Maui were equivalent to 3 kg/ha for the pre-reef count in 1962 and 249 kg/ha for the post-reef count (Hawaii DLNR 1967, 1973).

By comparison, fish densities estimated from fish-counting transects in areas without artificial reefs were much lower. For example, in Kealakekua Bay, Hawaii, which has a relatively pristine environment, the densities ranged from 65 kg/ha to 750 kg/ha and averaged 245 kg/ha. This average is probably low as it reflects a bias due to positioning transects over sandy areas where fish are scarce. At Honaunau Bay, Hawaii, the count was equivalent to a density of 254 kg/ha and off Waikiki, Oahu, the density was 166 kg/ha. The highest fish density recorded in the Hawaiian Islands was off the island of Niihau, where pristine conditions exist. Here, the mean count was 308 kg/ha over a transect located on a substrate particularly favorable for fish (Doty et al. 1968).

In Northwestern Hawaiian Islands waters, carangids, snappers, and groupers offer good potentials. Fourteen exploratory fishing stations with handline yielded good catches of white crevally, Carangoides ajax, thick-lip crevally, Caranx cheilio, pink snapper, Pristipomoides microlepis, amberjack, Seriola dumerilii, and sea bass, Epinephelus quernus (cruise report, "Townsend Cromwell," cruise 67, 20 October-26 November 1975). Good catches were obtained near Gardner Pinnacles where 11 C. ajax totaling 181 kg were taken and at Laysan Island where 33 C. ajax weighing 293 kg were captured in 3 h of fishing with five handlines.

Among other fishing methods used to assess the fish resources in Northwestern Hawaiian Islands waters, trawling is potentially one of the most important, particularly over the numerous banks and seamounts. The Soviet and Japanese seamount trawl fisheries appear to be relatively well established, although, as mentioned earlier, there is some evidence of a decline in armorhead catches. Exploratory trawling, conducted by the "Townsend Cromwell" (cruise report, "Townsend Cromwell," cruise 67, 20 October-26 November 1975), demonstrated that at Middle Bank, which is 62 m below surface, there were sizable concentrations of three species of acanthurids, Naso brevirostris, N. hexacanthus, and N. lopezi, a small serranid, Caesioperca thompsoni, and an introduced lutjanid, Lutjanus kasmira. Catch rates ranged up to 110 kg/h for Naso spp., 129 kg/h for C. thompsoni, and 41 kg/h for L. kasmira. Four daylight hauls at Middle Bank yielded from 33 to 230 kg, which when extrapolated indicate catch rates of 44-414 kg/h or an average of 242 kg/h. Assuming an effective trawl sampling width of 11.5 m using a "Norwegian" trawl with a 19.2-m headrope and an 25.3-m footrope, the standing biomass at Middle Bank was calculated to be 855-8,137 kg/km^2 or an average of 4,680 kg/km^2. These values compare favorably with estimated densities of demersal stocks in the region of the South China Sea, which range from 1,250 to 5,000 kg/km^2.

Five trawl stations occupied by the "Cromwell" north of Nihoa also yielded good catches. The catches, which varied from 83 to 158 kg/h and averaged 117 kg/h, indicated a standing biomass of 1,011-2,074 kg/km^2. Catches at Nihoa Bank, which is relatively shallow at 48-55 m, were dominated by N. brevirostris, N. hexacanthus, and Acanthurus olivaceus.

At a depth of 29-48 m near Necker, two daylight hauls by the "Cromwell" yielded relatively poor catches. A single night tow, however, produced a catch equivalent to a rate of 512 kg/h and to a standing biomass of about 8,028 kg/km^2. Although a variety of species was caught at this location, N. hexacanthus was again the dominant species. Trawl catches from deeper areas around Necker were very poor as were those made at St. Rogatien Bank.

Fish and shrimp traps also have been fished experimentally in waters of the Northwestern Islands. Snapper, locally called "opakapaka," were caught in fair numbers on four occasions in traps fished at the shelf edge north of Necker in 44-57 m of water. Catches ranged from 4.5 to 7.7 kg/set and averaged 5.4 kg. Near Kure, one trap, fished at 48 m produced 18.4 kg of Caranx cheilio. Two of 12 traps fished at Lisianski produced 16 and 48 kg of Carangoides ajax.

Surveys of the nearshore fishery resources also have been conducted in waters of the Northwestern Hawaiian Islands by the Hawaii Division of Fish and Game (narrative report, "Townsend Cromwell," cruise 76-04, 3 May-9 June 1976). Surveys around Nihoa, French Frigate Shoals, Laysan, and Necker showed that the carangids and sharks were relatively large compared to those found in waters of the major Hawaiian group and also more numerous. Members of the families Chaetodontidae, Apogonidae, Pomacentridae, Muraenidae, Holocentridae, and Acanthuridae, commonly associated with similar habitats in waters of the major Hawaiian group, were noticeably absent near the islands surveyed.

Fish counting transects demonstrated that densities were highest at Whale-Skate Island in the French Frigate group. Here, the estimated density averaged 4,744 kg/ha with goatfish, Mulloidichthys samoensis, C. ajax, and parrotfish, Scarus perspicillatus of major importance (Table 9). The lowest density occurred at Nihoa where the average was only 165 kg/ha with the pomacentrid, Chromis ovalis, and surgeonfishes, Ctenochaetus strigosus and Naso lituratus, the most predominant species.

Table 9.--Results of fish counting transects.

Location	Number of fish species	Estimated densities (kg/ha)	Major fish species ranked in terms of greatest densities
Nihoa Island	26	165	1. Chromis ovalis 2. Ctenochaetus strigosus 3. Naso lituratus
French Frigate Shoals			
East Island	29	2,219	1. Scarus perspicillatus 2. Kyphosus cinerascens 3. Mulloidichthys samoensis
Whale-Skate Island	32	4,744	1. Mulloidichthys samoensis 2. Carangoides ajax 3. Scarus perspicillatus
Laysan Island	34	848	1. Scarus perspicillatus 2. Acanthurus triostegus (= A. sandvicensis) 3. Thalassoma purpureum (= T. umbrostigma and T. fuscum)

In terms of species density, *M. samoensis* reached 2,206 kg/ha but *S. perspicillatus* was only slightly lower at a density of 2,183 kg/ha. When numbers of individuals were examined, however, the small round herring, *Spratelloides delicatulus*, was most numerous, occurring at a rate of 123,500 individuals/ha (Table 10).

Table 10.--Ten species of fish observed during underwater fish counting transects, ranked by estimated densities and number of individuals counted (narrative report, "Townsend Cromwell," cruise 76-04, 3 May-9 June 1976).

Estimated densities

Rank	Common name	Scientific name	Density (kilograms per hectare)	Occurrence (number of stations)
1	Weke-'a'a	*Mulloidichthys samoensis*	2,207	3
2	Uhu uliuli	*Scarus perspicillatus*	2,183	3
3	White ulua	*Carangoides ajax*	1,145	1
4	Nenue	*Kyphosus cinerascens*	626	4
5	Kala	*Naso unicornis*	430	4
6	Manini	*Acanthurus triostegus* (= *A. sandvicensis*)	420	4
7	Hinalea	*Thalassoma purpureum* (= *T. fuscum* and *T. umbrostigma*)	170	3
8	'Omilu	*Caranx melampygus*	143	3
9	Hinalea luahine	*Thalassoma ballieui*	95	4
10	White banded maiko	*Acanthurus leucopareius*	91	4
		Number of individuals		
1	Piha	*Spratelloides delicatulus*	123,500	2
2	Weke-'a'a	*Mulloidichthys samoensis*	2,485	3
3	Manini	*Acanthurus triostegus* (= *A. sandvicensis*)	590	4
4	Nenue	*Kyphosus cinerascens*	548	4
5	Uhu uliuli	*Scarus perspicillatus*	445	3
6	Kole	*Ctenochaetus strigosus*	267	4
7	Hinalea lau-wili	*Thalassoma duperreyi*	259	3
8	Blue damselfish	*Chromis ovalis*	247	1
9	Kala	*Naso unicornis*	242	4
10	'Omaka	*Stethojulis balteata* (= *S. axillaris* and *S. albovittata*)	185	2

6.4.5 Line Islands

Christmas Island, in the central equatorial Pacific, has been suggested as a possible site for a sport fishing resort. Helfrich (1973), who studied the feasibility of brine shrimp, *Artemia salina*, production on the island, recognized the potential for sport fishing resort development. Christmas Island, according to Helfrich, offers not only superb light-tackle fishing for bonefish and jack crevally but also ocean trolling for other game fish including yellowfin and skipjack tunas, wahoo, mahimahi, billfish, barracuda, and shark. Twenty-five and a half line hours of trolling yielded 42 fish totaling 361 kg or an average of 1.65 fish/line hour. In bottom fishing off the outer reef, catches varied from only a few red snappers, *Lutjanus bohar* and *L. gibbus*, per night to about 120 fish/h.

6.4.6 New Caledonia

Experimental deepwater handline fishing in New Caledonia, concentrated primarily on snappers and groupers at depths between 120 and 400 m, demonstrated that Pristipomoides flavescens were widespread at depths of 150-300 m and P. filamentosus occurred in large schools at depths as shallow as 30 m but usually down to 280 m (Fourmanoir 1973). Also found were P. sieboldi, usually caught at depths beyond 180 m and P. typus, a rather large snapper which were plentiful at depths of 190 and 210 m. Snappers of the genus Etelis were also caught but usually at greater depths. Etelis carbunculus usually occurred at 230-350 m whereas E. oculatus were found deeper at 400 m. Groupers, Epinephelus compressus, E. morrhua, and E. chlorostigma, were also prominent in the catches with E. compressus occurring in some abundance at 290 m.

6.4.7 Papua New Guinea

Based on current production, Wilson (1976) projected catches of several species groups from Papua New Guinea's waters in 1982 as follows: tuna - 68,000 MT; shrimps - 1,630 MT, lobsters - 360 MT; barramundi - 450 MT; baitfish - 1,360 MT; crabs - 180 MT; coastal species - 27,220 MT; and miscellaneous - 20 MT.

Studies conducted in Papua New Guinea indicate that, at present, there is no danger to any of the stocks fished, but barramundi catches may be close to the maximum sustainable yield and a major increase in fishing effort for this species will be discouraged (FDNIDA 1976). The lobster catch in the Daru reef area could be significantly increased without damage to the stock. Other studies have shown that marketable sharks and threadfins, Polydactylus sheridani and Eleutheronema tetradactylum, are abundant and could withstand increased harvesting. Lack of accurate statistics in the shrimp fishery prevents the formulation of suitable guidelines, but some control measures, particularly in the amount of fishing effort, will probably be adopted and modified as more accurate statistics become available.

Mixed reef-fish catches are not recorded accurately, but because coral reefs extend around most of the coast, the total production could be substantial. Offshore, in addition to skipjack tuna, small stocks of longtail tuna, Thunnus tonggol, are available but perhaps 1,000 MT would be its limit.

6.4.8 Solomon Islands

Among the options being considered for development in the Solomon Islands are fisheries for gem coral and deepwater demersal fishes. Initial results of a gem coral survey were inconclusive but further explorations are being planned (James 1977b). Offshore deepwater handline fishing surveys have indicated excellent catches of several tons per day of demersal fishes and, according to James, could possibly become an alternate fishery to the skipjack tuna pole-and-line fishery and gem coral harvesting. New fishing techniques are also being tried--bottom longlining and tangle netting have aroused keen interest among the local fishermen.

6.4.9 Tonga Islands

The prospects for developing fishery resources in the Tonga Islands appear to be extremely good because of the extensive shallow-water areas available to the fishermen (Wilkinson 1977b). The fishing grounds are all within cruising range of 30-40 fishing boats ranging in size from 9 to 12 m. In these shallow waters, the demersal stock, composed mainly of lethrinids and lutjanids, undergoes distinct seasonal migrations involving distances of up to 150 km between coral reef systems. Exploratory handline fishing has yielded catches dominated by Lethrinus lentjan, L. miniatus, L. variegatus, Pristipomoides typus, P. argyrogrammicus, and Cephalopholis sp. (Lorimer and Maclean 1974).

Initial trials with the Japanese fixed trap net (teichi-ami) have also been highly successful in Tongan waters (Wilkinson 1977a). One trap, fishing continuously at Pangaimotu near Tongatapu, produced 6.5 MT of several species of fish including T. crumenophthalmus, Harengula ovalis, Dussumiera sp., and Decapterus sp. Of these, Wilkinson considered 53.2% were of suitable size as live bait for skipjack tuna fishing, whereas the larger fish had a ready market among the local residents.

Fishery development projects also include establishment of a market infrastructure--cold storage facilities, transport, and introduction of modern, dory-type dual purpose fishing boats, which would be used to exploit pelagic species such as tunas when seasonally abundant and demersal species in the off-season for tuna (Wilkinson 1974).

6.4.10 Trust Territory of the Pacific Islands

The success of the dory project in American Samoa prompted other island governments in the Pacific to investigate the possibility of initiating similar projects. Among them was Ponape's Community Action Agency which launched a dory-building project by constructing a dory boat works in 1971. By 1973, the agency had constructed and launched eight dories which were designed for trolling and handline fishing nearshore (Perez and Sablan 1974).

The dories presently operating are 7.5 m long, equipped with citizen-band radios, and inboard Ford[4] engine with Hamilton jet pump. Among the fishes caught by trolling were skipjack and yellowfin tunas, wahoo, marlin, mahimahi, rainbow runner, dogtooth tuna, and other offshore pelagic species. Reef and bottom fishes caught by handlining or spearfishing included grouper, snapper, parrotfish, and jack crevally.

Data on fishing effort, catch, and catch per effort for the Ponape dory fleet for March 1973-March 1974, showed that during this period, 443 trolling trips for tuna and tunalike fishes produced 38.3 MT or an average of 85.6 kg/trip. Sixty-four handlining and spearfishing trips yielded only about a tenth of the trolling trips or 3.9 MT of reef fishes for an average of 60.5 kg/trip. Monthly indices of apparent abundance of tuna and tunalike fishes tended to be high in July, August, and October and low during other months of the year.

In surveys conducted in the Yap District, trolling gear, usually used when weather condition did not permit bottom fishing, produced catches of dogtooth tuna, wahoo, green snapper, Aprion virescens, barracuda, and small amounts of yellowfin tuna. Catches were relatively good in the passes of the larger atolls and along submerged reefs and banks at the 21-36 m depth contours. On days with good catches, for example, McCoy (1977) reported that up to 454 kg of dogtooth tuna were caught. In February-April 1976, catch of troll-caught species varied from 159 to 227 kg/day. In experimental handline fishing from skiffs, catches of red snapper (mostly Lutjanus bohar) and jack crevally varied from 122 to 272 kg/day/skiff.

6.4.11 Tuvalu

In 1976, a project to survey the outer-reef fishery resources around Tuvalu got underway. Fishing with handline for bottom fish along the outer slope of the barrier reef was very disappointing. Because of the steepness of the outer slope, the dory used in the bottom fishing survey encountered difficulty anchoring over the drop-off. To hold the dory in place over the fishing ground, an anchor was lowered in shallow water and enough warp paid out to fish over the desired depth. This was possible, however, only if the wind remained constant and blew offshore. Deepwater species such as Ruvettus sp., Etelis sp., and Pristipomoides sp., which were the major target species of the survey, occurred in well-defined depth ranges. Night fishing usually proved to be more productive than day fishing (Eginton 1977).

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[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

In 62 days of trolling and bottom fishing conducted by two dories in September-November 1976, 180.5 kg of pelagic fishes were caught by trolling and 2,417.5 kg of bottom fish by handline. The catch from troll and bottom gear reached 2,598 kg or an average of 41.9 kg/day. Ruvettus pretiosus constituted the largest proportion of the catch, by weight, accounting for 14% whereas lethrinids (13%), L. bohar (12%), and Katsuwonus pelamis (11%) were also important in the catch.

A small-craft evaluation project was also begun to assess the type of boat and engine most suitable for Tuvalu's fishermen (South Pacific Commission 1977c). Studies showed that trolling was economically feasible because of the presence of a substantial tuna resource on grounds that were readily accessible to small-craft operation. Gill-netting experiments also proved that a low-cost, small-craft fisheries could be a viable enterprise as catches by local fishermen proved profitable. And fishing for flyingfish demonstrated possible catches of up to 30 kg/h.

Because of the short time involved in the Tuvalu outer-reef fishing survey, data were insufficient to attempt even a preliminary evaluation of the fish resources. Reports from the local troll fishermen and from the survey staff indicate, however, that the skipjack tuna stock off the atoll appear to be quite substantial. More observations are necessary to obtain an index of school density in space and time. Deepwater fish resources, on the other hand, appear to be quite limited because of the very narrow band of shelf area just outside the barrier reef. Furthermore, there are no off-lying banks and seamounts rising sufficiently close to the water surface to support a possible offshore fishery. The fish resources of the lagoon appear to be underexploited at the present time, but because the lagoon area is only about 260 km^2, it appears doubtful that the lagoon fisheries could be expanded or support anything other than one at a subsistence level for local consumption.

6.4.12 Wallis and Futuna Islands

It was not until the latter part of 1970 that the government, through their Department of Rural Economy, set up a boat-building center to train the local natives in boatbuilding (South Pacific Commission 1977b). The dory and flat-bottomed skiff, both widely used in Canada, Newfoundland, and along the United States Atlantic coast, were selected as most suitable for local use. These crafts were seaworthy, economical to operate, and well-adapted to local, small-scale fishing needs. By the end of 1974, 80 crafts were in operation.

Because the lagoon fishery resources were seriously depleted by dynamiting and plant-poison method of fishing, it soon became evident that still larger crafts were needed to fish the outer-reef resources. Construction of several 8-m St. Pierre dories began in 1974. By 1976, the fishing fleet of small and large dories, skiffs, and marine plywood canoes reached 115 crafts. Demand for fishing crafts remains strong as more of the islanders return to sea to obtain fresh fish for their villages. The Department of Rural Economy anticipates yearly boat production to be maintained at about 10-15 small and 2-3 large crafts. Also included in the fisheries plan are construction of insulated ice chests and installation of an ice-making machine.

6.4.13 Western Samoa

A demonstration team of two boats with outboard motors and each manned by two fishermen taught fishing techniques in Western Samoa for an 11-mo period (Gulbrandsen 1977). The results demonstrated that an 8.5-m boat operated by an experienced crew can catch up to 10 MT of bottom fish in about 115 trips per year.

Two types of fishing crafts were deemed sufficiently seaworthy to remain at sea for night fishing and also provide reasonable comfort in the choppy waters often encountered around Samoa. One was a catamaran-type boat, a modified version of the local double-hulled canoe but built of pressure-treated marine plywood. The other was an 8.5-m, 20-hp, diesel-powered boat averaging speeds of 9 knots.

Data that can be used for resource assessment of outer-reef bottom fishes are practically nonexistent. For comparison, however, the catch rate of 3 kg/reel-hour, achieved by bottom fishing in Samoan waters, is less than half of the 6.8 kg/reel-hour obtained by the UNDP/FAO Carribean Fishery Development Project. Gulland (1971) estimated that the potential yield for groupers and snappers in the Carribeans is 2-10 kg/ha, similar to figures in other less productive parts of the world. Gulbrandsen, applying a catch rate of 0.5 MT/km^2 and a shelf area of 2,000 km^2 for Western Samoa, estimated that the annual potential catch of bottom fish could reach 1,000 MT. (The depth to which the shelf area was estimated is not given.)

The Government of Western Samoa has also embarked on upgrading the existing fishing fleet. Traditional fishing canoes, once the foundation of the island's nearshore fishing fleet, are rapidly being replaced by catamaran-type and diesel-powered boats. In 1976, Philipp (1977) estimated that the Western Samoan fleet of 160 small, miscellaneous boats of under 2 tons carrying capacity caught a wide variety of fish totaling 500 MT. An additional 200 MT were taken by net and spear fishermen primarily inside the reef.

6.5 Crustaceans

Crustaceans constitute only a minor proportion of the Hawaiian catch. Presently, the species exploited include spiny lobsters, *Panulirus marginatus* and *P. penicillatus*, squat lobster, *Scyllarides squammosus*, shrimp, *Penaeus marginatus*, kona crab, *Ranina serrata*, white crab, *Portunus sanguinolentus*, red crab, *Podophthalmus vigil*, and mangrove crab, *Scylla serrata*. The gear most commonly used to capture crustaceans include traps, anchor nets, and lift nets. Yaldwyn (1973) estimated that there are at least 450 species of decapod crustaceans in Hawaiian waters.

The decapod crustacean fauna of South Pacific reefs and islands probably total somewhere between 400 and 800 species (Yaldwyn 1973). The two most strongly represented families in the South Pacific region are the snapping shrimps, Alphaidae, and the dark-fingered crabs, Xanthidae. Other well represented and ecologically important groups include the commensal and freshwater shrimps, Palaemonidae, the large spiny lobsters, Palinuridae, the nocturnal land hermit crabs, Coenobitidae, and the related land crab, Gecarcinidae, the swimming crabs, Portunidae, and the shore crabs, Grapsidae, most of which are important as food. Yaldwyn suggested that based on a mid-figure of 600 species, there are at least 150 species of shrimps, 325 species of crabs, and 125 others. The decapod fauna of the South Pacific region is part of that within the Indo-Pacific region and shows strong attenuation in genera and species from west to east.

6.5.1 Frog crab

Of the 33 MT of crustaceans caught in Hawaiian waters, kona crab is usually the most important, constituting about a third and sometimes up to three-fourths of the landings (Table 11). Virtually the entire catch of kona crab is taken over sandy bottom in waters which range from less than 6 m up to 90 m in depth. Onizuka (1972) has shown that a large proportion of the catch comes from Penguin Banks off the western coast of the island of Molokai; the northern coastal waters off Niihau is next in importance. Knowledge of the resources of this species throughout the rest of the major Hawaiian Islands is relatively poor.

Catches of this species in 1961-72 rose from 4 to 33 MT but declined in subsequent years and by 1975, only 8 MT or about one-fourth of the 1972 catch was reported.

Regulations presently in effect prohibit capture of ovigerous females and marketing crabs with carapace width or length of less than 10.2 cm. The regulation on size, however, does not afford the protection intended for the immature crabs, because those that are undersized are taken for home consumption (Onizuka 1972).

Catches of white crab in Hawaiian waters, which have also shown an upward trend in recent years, varied between 1 and 4 MT in 1961-68, but rose to higher levels and fluctuated between 10 and 26 MT in 1969-75.

Table 11.--Nominal catches of marine crustaceans, marine crabs, lobsters, shrimps and prawns, molluscs, and marine shells in western central Pacific islands (in metric tons) (FAO 1970, 1975c, 1976b).

	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
Marine crustaceans											
Cook Islands	00	00	00	00	00	00	00	00	00	0	0
Fiji Islands	--	--	--	--	--	--	--	--	100	188	196
New Caledonia	100	100	100	100	100	100	100	100	200	268	250
Marine crabs											
Hawaiian Islands[1]	13	12	14	21	29	39	46	52	37	44	25
Papua New Guinea	--	--	--	--	--	--	--	--	--	150	450
Lobsters											
American Samoa	00	00	00	00	00	00	--	--	--	1	--
French Polynesia	--	--	--	--	--	00	00	00	00	0	2
Hawaiian Islands[1]	4	2	2	2	4	3	3	2	3	2	--
Papua New Guinea	--	--	--	--	--	--	--	--	--	340	265
Trust Territory of the Pacific Islands	--	--	--	--	--	--	00	00	00	5	5
Shrimps and prawns											
French Polynesia	00	00	00	00	00	00	00	00	00	0	0
Guam	--	--	--	--	--	--	--	--	--	--	0
Hawaiian Islands	<1	<1	<1	<1	<1	1	1	<1	<1	2	3
Papua New Guinea	--	--	--	--	--	--	300	800	1,000	668	417
Trust Territory of the Pacific Islands	--	--	--	--	--	--	00	00	00	0	0
Molluscs											
Cook Islands	600	600	600	600	600	600	600	600	600	600	600
Hawaiian Islands[1]	11	19	16	16	13	16	17	14	21	14	14
New Caledonia	200	200	00	00	00	00	00	00	00	0	0
Marine shells											
Fiji Islands	--	--	--	--	--	--	--	500	600	271	320
French Polynesia	--	--	--	--	--	00	100	100	00	0	0
New Caledonia	100	100	00	00	00	00	00	00	00	0	0
Papua New Guinea	300	300	400	400	400	400	--	--	--	--	--
Solomon Islands	--	--	--	--	--	--	--	--	--	317	534

00 = More than zero but less than 50 MT.

0 = More than zero but less than 0.5 MT.

[1] Data are from Hawaii Division of Fish and Game, commercial fish catch, by species, 1965-75, mimeo.

6.5.2 Spiny lobsters

Whereas the commercial catch of spiny lobsters in Hawaii has declined significantly from nearly 60 MT in 1900 (Morris 1968) to about 2 MT in 1974, surveys show that there are probably unfished resources of spiny lobsters at depths not fished by present methods in waters around not only the major Hawaiian Islands but also around the Northwestern Hawaiian

Islands. In 1965, scientists in a small research submarine, explored the ocean bottom to depths of 183 m off the coast of Oahu and observed rather large quantities of spiny lobsters at depths between 24 and 107 m (Strasburg et al. 1968). From one small viewing port, about 70-80 lobsters were seen. At 107 m, about 20 lobsters were crowded in a small cave. The largest of these lobsters was estimated to be about 3.2 kg in weight as compared to 0.5-0.9 kg of an average reef-caught lobster.

Experimental fishing with the 1.5 x 1.5 x 1.2 m and the 0.6 x 0.6 x 1.2 m traps for the spiny lobster, Panulirus marginatus, showed that catches from various locales within the Northwestern Hawaiian Islands were quite variable (Uchida and Hida 1977). For example, the best catches occurred off Necker Island where 17 traps fished at 27-57 m produced 160 lobsters or an average of 9.4 lobsters/trap. Here, the average size reached 0.6 kg. Traps fished near the edge of the bank in 44-57 m of water produced the best catches. At a station north-northwest of Nihoa Island, 11 traps, fished in 44-48 m of water produced 41 lobsters or an average of 3.7 lobsters/trap, weighing an average of 0.9 kg each. Catches were relatively poor at stations occupied near Pearl and Hermes Reef, Kure Island, Lisianski Island, Laysan Island, and Gardner Pinnacles. The commercially valuable kona crab occurred in traps set in 46-55 m of water off Pearl and Hermes Reef and Kure Island. Three traps at Kure produced 4.5-27.2 kg/trap or an average of 13.9 kg/trap.

Fishing with the 1.5 x 0.9 x 0.6 m Hawaiian trap and the 0.9 x 0.6 x 0.4 m California two-chambered lobster pots on another cruise also yielded good catches of spiny lobsters around Necker Island. Among six sets made during the cruise, one set produced a spectacular 428 lobsters. At this particular set, the Hawaiian traps produced 229 lobsters or an average of 19.1/trap. The California pot, being much smaller in size and total volume, yielded 199 lobsters or an average catch of 16.5/trap. The maximum catch at one station, consisting of a string of four traps, was 106 lobsters or an average of 26.5/trap. For individual traps, one Hawaiian trap yielded a maximum of 49 lobsters while the maximum for a California pot was 33 lobsters.

In the Gilberts, commercial concentrations of spiny lobsters, P. penicillatus, have been reported from many of the islands in the group, but development of this fishery has been delayed because of problems involved in transporting live lobsters from the place of capture to the markets (Gibson 1975). Experiments on live storage indicated that feeding during storage and transporting did not reduce mortalities significantly and that lobsters fed daily and transported in wet or dry sawdust had a higher survival rate than unfed ones transported in wet jute sacking, particularly for journeys longer than 8 h (Prescott 1977).

The commercial development of the Papua New Guinea spiny lobster, Panulirus ornatus, fishery, which began in 1961-62 with establishment of shoreside cold storage and processing facilities at Yule Island, has been described by Pyne (1970), George (1972), and Wilson (1976).

Briefly, fishing from small canoes or dinghies, either towed to the grounds by 7-m diesel-powered dories or with sail, takes place over shallow reef tops at night with the use of kerosene lamps and pole nets and during the day by divers using surround nets, spears, and tangle nets.

At Yule Island, because the fishery depends on seasonal migration of spawning aggregation of P. ornatus, major fluctuations occur in annual landings. At Daru reefs, however, the fishing is not seasonal. Studies indicate that the Daru reefs stock is not a local population but part of a much larger migratory population, which continuously restocks the reefs as it moves north from the large reef complexes in Torres Strait (FDNIDA 1976; Moore and McFarlane 1977).

Spiny lobsters in Papua New Guinea are also taken by trawlers. This fishery began in 1973, and is active from August to December when the lobsters migrate and captures the largest proportion from Papua New Guinea waters. Of the larger trawlers (>20 m), 24 fished for lobsters in 1973 and 1974, but the number declined to 4 in 1975 and 12 in 1976.

6.5.3 Shrimp

In 1967-68, the National Marine Fisheries Service's research vessel, "Townsend Cromwell," surveyed 4,974 km^2 of bottom area in Hawaiian waters and found 2,106 km^2 trawlable, 2,280 km^2 untrawlable, and 587 km^2 marginally trawlable (Yoshida 1972). One relatively large, uninterrupted area of trawlable bottom was located north of the island of Hawaii. One hundred and nineteen drags made with the Gulf of Mexico-type, flat shrimp trawl yielded penaeid shrimp, *Penaeus marginatus*, flatfishes, Bothidae and Pleuronectidae, spiny lobster, *Panulirus marginatus*, and white crab.

Yoshida reported that the shrimp, caught in depths between 27 and 234 m on sandy and sand-mud substrate, was the most promising species for the development of a commercial fishery. The catches of this species, which ranged from 0.45 to 16.10 kg/drag, were always better at night than during daytime.

In attempts to capture *Penaeus marginatus* in Hawaiian and Northwestern Hawaiian Islands waters with other types of gear, Struhsaker and Aasted (1974) conducted deepwater shrimp trapping surveys. A total of 82 sets involving 306 traps and 3,960 h of fishing time in the 135-825 m depth range yielded poor results. More success, however, was experienced in trapping caridean shrimps, *Heterocarpus ensifer* and *H. laevigatus*. For these caridean shrimps, burlap cloth-covered traps outfished uncovered traps by factors of 2.5 to 10.

Heterocarpus ensifer was most abundant in depths of 365-455 m where catches ranged from 6.8 to 28.6 kg/trap for sets of less than 24-h duration. The larger *H. laevigatus* was abundant in deeper waters ranging from 440 to 685 m where catches ranged up to 15.8 kg for four traps.

Struhsaker and Aasted indicated that traps are a much more efficient means of harvesting *H. ensifer* in Hawaii and concluded that an annual yield of 1 or 2 MT/km^2 for Hawaiian waters does not seem like an unreasonable estimate. The total area of optimum depth range for *H. ensifer* within the major Hawaiian Islands has not been precisely determined but probably exceeds 1,000 km^2.

Comparison of catch rates for *H. ensifer* showed that in the western Atlantic, exploratory trawl catches by the NMFS were of the same magnitude as those in Hawaiian waters (Struhsaker and Aasted 1974). Limited trapping experiments near Guam in the western Pacific also produced catches similar to those in Hawaii. Struhsaker and Aasted speculated that *H. ensifer* and other members of this genus represent an unexploited resource of considerable magnitude.

Scientists aboard the "Townsend Cromwell" also surveyed waters of the Northwestern Hawaiian Islands with a 12.5-m headrope, semiballoon shrimp trawl at depths of 29-37 m and in deeper waters ranging from 400 to 785 m. Catches were small; the deeper hauls produced the caridean shrimps, *H. ensifer* and *H. laevigatus*, at the rate of 0.7-0.9 kg/h.

Papua New Guinea's shrimp fishery, concentrated in waters less than 55 m (30 fathoms) along the coast in the Gulf of Papua and the western provinces, is based on three species--banana shrimp, *Penaeus merquinensis*, the endeavour shrimp, *Metapenaeus endeavouri*, and the tiger shrimp, *P. monodon*. The fishery is seasonal, primarily from March to July with much of the fishing occurring in the Gulf of Carpentaria. In January-February endeavour shrimps are plentiful off Kikori, whereas from March to July, banana and endeavour shrimps occur in the Gulf of Papua but are most abundant off the mouth of the Fly River and Kerema. In 1976, Wilson (1976) reported that the trawling fleet consisted of four 100-250 GT (gross tons) and three 15-m single-rigged shrimp trawlers based at Port Moresby. Two other trawlers operated out of Yule Island.

6.6 Molluscs

In Hawaii, there are several large beds of American oysters, *Crassostrea virginica*, in

West Loch, Pearl Harbor. According to standards established by the U.S. Public Health Service for oyster growing waters, the estuarine waters of Pearl Harbor are grossly polluted; therefore, no harvesting of oysters is permitted. The Hawaii Division of Fish and Game, nevertheless, actively pursues research in oyster culture. In 1962, there were 19 major beds in West Loch containing about 36 million live oysters (Hawaii DLNR 1971; Kawamoto and Sakuda 1973). The total area of the beds, which was estimated to be 125,400 m^2 in 1962, increased to an estimated 175,600 m^2 by 1971, an increase in culturing area of about 40%. The number of live oysters, on the other hand, decreased during this period by about 3%; however, the larger sizes of oysters encountered in 1971 resulted in a 127% increase in estimated production to 126,459 bushels.

Kawamoto and Sakuda (1973) determined that oysters attain maturity at 2 mo and legal harvesting size at 15 mo in West Loch. The annual mortality rate was estimated at 68.7%. Studies also showed that oysters increased from a subcommercial quality (condition index 6.1) to a commercially acceptable quality (condition index 8.0) in 3 weeks by using an artificial feeding regime. A depuration experiment demonstrated that oysters previously in a restricted area could be cleansed within 1 week to an acceptable condition for marketing.

Reported landings of molluscs in the Hawaiian Islands, which averaged about 15 MT in 1961-75, are lower than the actual catch, but it is difficult to estimate the unreported landings of the recreational fishermen. Nearly 60% of the reported catch is composed of limpet, Cellana exarata and C. sandwicensis, locally called "opihi," whereas the remainder of the catch consists of octopus, Polypus marmoratus and P. ornatus, and squids, mostly Notodarus hawaiiensis. Harvesting of clams, Venerupis philippinarum, is regulated by the Hawaii Division of Fish and Game and is usually allowed for 3 mo--September-November--after it has been determined that clams are sufficiently abundant to allow fishing and provided that waters in the clamming grounds have been declared free of bacterial contamination.

In French Polynesia, one of the important fisheries is that for blacklip pearl shell, Pinctada margaritifera. Because of the heavy fishing pressure exerted by pearl shell divers, government regulations have been instituted to protect the resources of pearl shell (Van Pel 1961). Each year, some lagoons or sections of lagoons are opened for pearl shell harvesting once every 4 yr. A minimum size regulation is also enforced. Each lagoon includes one reserved area where absolutely no harvesting is permitted.

In 1957, Trochus niloticus was introduced on reefs of Tahiti from New Caledonia. The success of these plantings have resulted in the establishment of a fishery where methodical harvesting is allowed (Doumenge 1973). Harvesting is strictly supervised through a special ordinance of the Governor of French Polynesia.

Harvested in large quantities by the local residents in Tonga are arc shell, Andara maculosa, which comprises nearly 50% of the shellfish sold, giant clams, Tridacna gigas and T. maxima, up to 45 cm long, small scallops, blacklip pearl shell, venus shell, and thorny oyster, Spondylus sp. Popular gastropods include spider shell, Lambis lambis, tiger and egg cowries, Cypraea tigris and Ovula ovum, various species of Murex, and the triton, Charonia tritonis (Lorimer and Maclean 1974).

6.7 Echinoderms

Sea urchins and, in particular, sea cucumbers form a very important segment of the bottom fauna within the coral reefs of many of the central and western Pacific islands. They also constitute part of the diet of many Pacific islands.

Bêche-de-mer formed the basis of a very prosperous fishery in the Pacific region before World War II. Truk Island in Micronesia, for example, exported 450 MT (20-30/yr) mostly to Japan during the period of Japanese administration prior to World War II (1914-41). Two world wars interrupted the growth and continued development of this fishery in Micronesia and New Hebrides, but there is growing interest among the Pacific islands government to revive it (Smith 1947; South Pacific Commission 1974). In Papua New Guinea, Solomon Islands, and Fiji, the fishery has made a modest revival in recent years.

Among the commercially exploitable species of sea cucumbers are teatfish, *Microthele nobilis*, blackfish, *Actinopyga miliaris*, deepwater redfish, *A. echinites*, surf redfish, *A. mauritiana*, stonefish, *A. lecanora*, pricklyfish, *Thelenota ananas*, sandfish, *Holothuria scabra*, leopardfish (tigerfish), *Bohadschia argus*, chalkyfish, *B. marmorata marmorata*, "Suthuwalu," *B. marmorata vitiensis*, lollyfish, *Halodeima atra*, and a species, *Stichopus variegatus*, which has no common name but is similar to the pricklyfish. According to FAO (1976b), catches of sea cucumbers in the Solomons were 200 MT in 1972 and 300 MT in 1973 but they declined sharply in 1974 and 1975 reaching only 18 and 9 MT, respectively. Catches from Fiji were very small reaching only 2 MT in 1974.

At present, the only processing plant for sea cucumbers in the Pacific region is located in the Solomon Islands. Here, four species are of commercial importance--teatfish, blackfish, pricklyfish, and deepwater redfish (James 1977a). In New Hebrides, several commercially important species are found in the lagoons and an active fishery could be organized in various parts of this island group. Fiji exports bêche-de-mer to Australia and the United States but the trade is not well organized. Palau in the Trust Territory has good prospects for the establishment of a bêche-de-mer fishery as large quantities of commercially important species are found inside the lagoon. At present, there is no obstacle to the reestablishment of this fishery in the Palau District. At Yap, however, the lagoon area is small and probably cannot support an active large-scale fishery.

Surveys conducted in Truk lagoon showed that teatfish and pricklyfish are abundant and can support an active fishery to command dominance in the Trust Territory (Sachithananthan 1972). The potential for development is extremely good and the sooner it is started, the firmer will be its foothold in Truk. On the other hand, teatfish and pricklyfish are rarely seen at Ponape, but sandfish and lollyfish are predominant. At Kwajalein in the Marshalls, several commercially important species are abundant and a fishery for them can be established by organizing the small groups of fishermen in each atoll.

7. CIGUATERA

Ciguatera fish poisoning, also known as ichthyosarcotoxism in medical terminology, is a disease with certain characteristic neurotoxic and gastroenteric symptoms produced by ingestion of a variety of fish including snapper, Lutjanidae, groupers, Serranidae, jacks, Carangidae, barracuda, Sphyraenidae, and surgeonfish, Acanthuridae, from toxic areas (Halstead and Lively 1954; Helfrich, Piyakarnchana, and Miles 1968). According to Helfrich et al. ciguatera and tetraodon poisoning can be distinguished from each other by the character of the toxin and symptomatology, and from scombroid poisoning by distinct etiological agents which have been isolated. Clupeoid poisoning also appears to be distinct from ciguatera fish poisoning on the basis of symptomatology. Recent evidence shows that ciguatera is probably caused by more than one toxin and includes what has been described as *Gymnothorax* poisoning and elasmobranch poisoning; the toxins from snappers, shark livers, and moray eels have been isolated and appear to be identical (Ralls and Halstead 1955; Halstead 1959; Banner et al. 1964).

Ciguatera appears to be widespread through the oceanic islands of the Pacific between the 30° parallels of latitude (Helfrich et al. 1968). Although the occurrence of ciguatera poisoning has a discontinuous distribution, the condition has been reported from at least some of the islands of all the archipelagoes of the tropical Pacific with the exception of the Carolines and the Philippines (Helfrich and Banner 1968). For an exhaustive review of investigations on ciguatera, the reader is referred to Halstead (1965-70). Abstracts of papers presented at a seminar on ichthyosarcotoxism may be found in South Pacific Commission (1968).

The occurrence of ciguatera in some species found in the central Pacific affects not only the population by causing illness, but also as is often the case, deprives them of a major source of protein. In some areas that are seriously affected, it could restrict the full development of an outer reef handline fishery and utilization of the demersal stocks. Table 12 gives the results of toxicity tests conducted on fishes caught in waters around the Line Islands.

Table 12.--Line Islands fishes tested for toxicity at Hawaii Institute of Marine Biology (Helfrich et al. 1968).

Family	Species	Results	
		Toxic	Nontoxic
Acanthuridae	*Acanthurus triostegus triostegus* (Linnaeus)	x	
	A. xanthopterus Cuvier and Valenciennes	x	
	Ctenochaetus striatus (Quoy and Gaimard)	x	
	C. cyanoguttatus Randall	x	
Albulidae	*Albula vulpes* (Linnaeus)		x
Carangidae	*Caranx ignobilis* (Forskål)	x	
	C. melampygus Cuvier	x	
Chaetodontidae	*Chaetodon auriga* Forskål		x
Elopidae	*Elops machnata* Forskål		x
Labridae	*Cheilinus undulatus* Ruppell		x
Lutjanidae	*Lethrinus miniatus* Bloch and Schneider	x	
	L. variegatus Cuvier and Valenciennes	x	
	Lutjanus bohar (Forskål)	x	
	L. monostigmus (Cuvier and Valenciennes)	x	
	L. gibbus (Forskål)	x	
	Monotaxis grandoculis (Forskål)	x	
Mugilidae	*Mugil crenilabis* (Forskål)		x
	Neomyxus chaptalii (Eydoux and Souleyet)		x
Muraenidae	*Gymnothorax javanicus* (Bleeker)	x	
Serranidae	*Anyperodon leucogrammicus* (Cuvier and Valenciennes)	x	
	Epinephelus fuscoguttatus (Forskål)	x	
	E. tauvina (Forskål)	x	
	Variola louti (Forskål)	x	
	Cephalopholis argus Bloch and Schneider	x	
Sphyraenidae	*Sphyraena barracuda* (Walbaum)	x	

In Tonga, ciguatera poisoning does not appear to be serious--a species which is usually suspect is *Lutjanus bohar*. At times, this species is excellent eating whereas in some months, it may affect the consumer (Wilkinson 1977a).

In Western Samoa, ciguatera poisoning also is not a serious problem. *Lutjanus bohar* which is the only species thus far implicated in poisoning cases, constitutes only 5% of the total catch (Gulbrandsen 1977).

The problem of ciguatera poisoning in the Yap District occurs only at Ulithi Atoll and only in certain sections. Species occasionally implicated in poisoning cases in other localities in the Pacific--barracuda, lutjanids, and large carangids--have not caused poisoning cases in Yap (McCoy 1977).

At Penrhyn in the northern Cook Islands, a recent increase in cases of fish poisoning has been attributed to a hurricane which struck the islands and caused widespread damage to the reef coral (Brandon 1976). It was suggested that a rapid increase in new corals could have initiated the sudden increase in ciguatera poisoning. Brandon stated that this theory is partially supported by the decline in incidence of fish poisoning cases with time following a peak shortly after the hurricane.

Among the fishes implicated in fish poisoning cases at Penrhyn were snappers, L. bohar and L. vaigiensis, coral cod, Cephalopholis miniatus, moray eel, Gymnothorax sp., red emperor, Lethrinus sp., white parrot, Scaridae, wrasse, Cheilinus undulatus, and surgeonfish, Ctenochaetus striatus.

Not all the deepwater fish caught in Tuvalu are salable. Ciguatera poisoning, although not a serious problem in Tuvalu, could have a detrimental effect on fishery development because of the relatively high proportion of poisonous fishes in the catch. Eginton (1977) estimated that about 17% of the survey project's fish landings were poisonous and included such species as L. bohar, Variola louti, Plectropoma maculatus, and other large groupers, and several unidentified lutjanids.

8. DISCUSSION

The high population growth rate in many of the Pacific islands over the past decade has had a significant effect on the pattern of fishing. In some islands, the tradition of fishing has practically been lost. For example, copra plantation operators encourage the local population to earn cash income through copra production and to obtain their fish through purchases at the plantation store (Murphy 1973). Thus, the ability to fish and the tradition of going to sea eventually is lost after a few generations of this type of pressure. Furthermore, fishing pressure on fish resources in the lagoons and adjacent reef and shallow-water areas has increased steadily resulting in serious depletion of some stock. In many cases, resources that have been the basis of subsistence fishing for generations no longer exist.

It has been suggested that among the species presently being harvested within the western central Pacific, skipjack tuna, together with other small tunas, will dominate fishery production (Wilkinson 1977b). It appears unlikely that a commercial fishery for any of the other species can compete. For example, even the deep-swimming tunas and billfishes are under considerable fishing pressure and production from these resources appears to be stabilizing so that substantial increases in catches of these species seem unlikely. This does not mean, however, that the coral reef and outer-reef fisheries do not have the potential for further development. On the contrary, because of the lifestyle of Pacific islanders, these small-scale fisheries will continue to have considerable socioeconomic value to the villages and communities in the region.

The coral reef environment can be harvested with indigenous and relatively uncomplicated fishing techniques that have evolved over the years (Wilkinson 1977b). And it is not likely that the traditional artisanal method of fishing will change drastically in the near future. The problem of estimating sustainable yield levels for coral reef communities, however, is formidable indeed because of the high degree of diversification. The wide variety of species harvested from this environment, coupled with local sociological factors that tend to inhibit proper utilization, will have a significant influence on rational long-term management of the coral reef resource. The economic factors also dictate, to some extent, the expenditure of fishing power; therefore, there will be some degree of management.

It has become abundantly clear in recent years that developmental effort in the future has to concentrate on introducing different methods of fishing to harvest the outer-reef slope and nearshore pelagic resources. The fisheries for these resources will surely emerge in the years to come, but their development will require new or perhaps untried and untested techniques. Among the urgent needs are powered fishing boats which can withstand the choppy offshore waters and also provide reasonable amount of comfort to the fishermen handling gurdies and other mechanical devices for bottom fishing in deep, outer-reef waters, refrigeration to preserve the catch, simple echo sounders, and training in simple navigation.

9. REQUIREMENTS FOR FURTHER STUDY

The preponderance of studies on fish resources has been concentrated in the North Pacific. For the period 1949-68, there were 202 papers dealing with biological oceanography of the North Pacific in contrast to only 18 on similar subjects for the South Pacific (Knox 1970). The main reason for this difference is that the countries engaged in the North Pacific fisheries are highly developed technologically resulting in higher allocations of funds for marine research.

In general, for almost every island or island group covered in this report, the prime requirement is for catch and effort statistics, which, at the present time, are usually incomplete, or, in the case of subsistence fisheries, nonexistent. To obtain any kind of statistical data in such a vast area with many relatively underdeveloped islands, however, presents many problems. For example, lack of communication between the government centers and outlying villages and lack of trained personnel amongst the villagers to record catch and effort data accurately, systematically, and consistently are two very basic problems that need immediate attention.

A considerable amount of work is also needed to better understand the biogeography in the central South Pacific. For example, information is very scanty on the distribution of plankton and benthic animals in the South Pacific. Other measures of biological productivity, such as primary production in the oceanic regions, as well as in the coral reef ecosystem, would be most useful. Estimates of relative abundance of planktonic eggs and larvae of important commercial species, with the exception of the tunas, are sparse and much could be done in this area.

Information on the outer-reef demersal and pelagic resources is also very sparse. Correspondingly detailed data on hydrography and bottom topography are also lacking from around most of the islands. It would appear, then, that apart from statistics, the most urgent need is for extensive surveys of the demersal and pelagic resources. A proposal to assess the marine resources of the Northwestern Hawaiian Islands has already been implemented by the Southwest Fisheries Center, National Marine Fisheries Service, Honolulu, Hawaii and preliminary results from some of these islands and atolls indicate the existence of possible commercial concentrations of demersal fish species and shellfish.

In most western central Pacific islands, there is no basis of past fisheries experience to indicate the size of the coastal and pelagic resources with much accuracy. Furthermore, detailed information about standing stocks or potential sustained yields from the shelf or coastal areas of the many Pacific islands, even in areas of high population density and high market demand such as the Hawaiian Islands, is almost completely absent. It is not expected that potential production from the many coastal areas of these islands, however extensive they may be, would be large enough to withstand the intense fishing pressure of industrial fisheries which occur in temperate coastal regions of the world. Nevertheless, the potential production is probably adequate or ample in many of these coastal areas to supply the local needs for many types of fishery products.

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7834

EFFECTS OF CHRONIC CONCENTRATIONS OF PETROLEUM HYDROCARBONS ON GONADAL MATURATION IN STARRY FLOUNDER (PLATICHTHYS STELLATUS [PALLAS])

Jeannette A. Whipple, Thomas G. Yocom,
D. Ross Smart, and Meryl H. Cohen
National Marine Fisheries Service
Southwest Fisheries Center
Tiburon Laboratory
Tiburon, California 94920

ABSTRACT

Adult starry flounder, during gonadal maturation, were continuously exposed to low concentrations (100 to 200 ppb) of the water-soluble fraction (WSF) of Cook Inlet crude oil for periods of 5, 7 and 21 days. Daily observations of behavior were made and fish were subsampled to determine effects on their gonads and other organs. Accumulations of low-boiling-point aromatic hydrocarbons were measured in the gonad and liver.

Female flounders accumulated a mean concentration of 12.98 μg/g (ppm) monocyclic, cyclohexane and dicyclic components in mature ovaries, 113 times the water column concentrations.

Several changes in behavior and histological damage in ovaries and livers were attributed to chronic doses of WSF. Egg maturation was accelerated and abnormal and dead eggs were observed in both immature and mature ovaries of exposed females. Maturation of male testes was also accelerated. Extensive vacuole formation was found in livers from exposed flounder.

If such effects also occur in the field at chronic levels, low concentrations of oil could have serious consequences on natural populations. If marine organisms prove generally to be more sensitive during their spawning season, fishery management decisions should consider timing of oil-related activities to adequately protect fishery resources.

INTRODUCTION

In recent years, oil spills and tanker accidents have shown a need for greater knowledge of the effects of oil on marine biota. Perhaps of greater concern than catastrophic incidents, however, is increasing chronic oil pollution, particularly in estuaries with continuous boat traffic, recurring minor spills associated with oil transport, and ongoing discharges of municipal and industrial effluents.

Estuaries are important habitats in the life histories of many fishes and sustain important commercial and recreational fisheries. Several species migrate into shallow waters off estuaries (e.g. starry flounder; Orcutt 1950) or through estuaries to spawn (e.g. salmon, striped bass). Estuaries are also important nursery areas for the young stages of many fish. Therefore, many species cannot avoid being exposed to chronic concentrations of pollutants during critical and sensitive life history stages.

Previous work at Tiburon Laboratory showed that prespawning Pacific herring were adversely affected by lower concentrations (100-800 ppb) of benzene than were egg and larval stages (which were adversely affected only at ppm concentrations). Adult herring exposed prior to spawning exhibited erratic spawning behavior, spawned prematurely, and suffered gonadal egg death. Survival of gonadal eggs and larvae to hatching and through yolk absorption was decreased by 50 percent (Struhsaker 1977).

The purpose of the experiments conducted and described here was to examine the effects of low concentrations of the WSF of Cook Inlet crude oil (approximating a chronic field concentration) on female and male starry flounder prior to spawning. An attempt was made to relate these effects to concentrations of the low-boiling-point aromatic and alkyl cyclohexane components accumulated in the gonadal and liver tissues; primary emphasis was given to the low-boiling point, monocyclic and dicyclic aromatic components of the water-soluble fraction (WSF) of crude oil because these components comprise a major portion (50-90%) of the water-soluble fraction (WSF) of several crude and refined oils (Anderson et al. 1974b) and are also relatively toxic.

METHODS

Fish:

Starry flounder, Platichthys stellatus (Pallas) were collected from inshore areas near Bodega Bay, California. Fish were captured with an otter trawl by personnel of the California Department of Fish and Game and were transferred to 1900-liter tanks at Tiburon for acclimation.

Flounder were not fully ripe when captured, and were in varying stages of maturation prior to spawning. Standard lengths, wet weights of adults, lengths and weights of gonads and other morphometric data of the fish used in the experiments are summarized in Table 1. The primary difference between experiments was in the percentage of adults with maturing gonads. In Experiment 1 (January) females were in earlier maturation stages. In Experiment 2 (February) most females were maturing and in late maturation stages; the males were all ripe. Throughout the experiments we were unable to obtain ripe-running females from the field, so in Experiment 3 (April) an attempt was made to induce spawning. This experiment was unsuccessful, because most females were in a refractory period (resting stage). Males, however, were ripe and some results from this experiment are reported.

Apparatus:

Three experiments were performed in a continuously flowing system using dosing apparatus developed by project personnel (Benville et al., manuscript in prep.). This apparatus (Figure 1) produced a stable outflow of the water-soluble fraction of Cook Inlet crude oil which could be diluted easily to desired concentrations.

Acclimation and Experimental Conditions:

Flounder were acclimated to experimental conditions for at least two weeks prior to experimentation. The experiments were conducted at ambient levels at the time of testing (Table 2). The mean temperatures for the three experiments were 10.7, 13.7, and 17.2°C, respectively. The flounder were fed a diet of squid and bay shrimp during acclimation.

Because they do not feed during spawning and the exposure periods were relatively short (5 and 7 days), flounder were not fed during the first two experiments. In Experiment 3, flounder were fed the last week of the exposure period.

Test groups of starry flounder were placed in each of two 866 liter fiberglass tanks; one tank received a continuous flow of WSF in seawater at a mean concentration from 115 to 221 ppb (depending upon which experiment, Table 2). The other tank received uncontaminated (control) seawater at the same flow rate.

Flounder were continuously dosed during experimentation. Water samples were taken and analyzed daily to determine the concentration of low-boiling-point hydrocarbons in each of the tanks and the dosing apparatus effluent. Temperature, salinity, oxygen, and flow rate were monitored daily.

Daily observations of behavior included ventilation rate (number opercular beats/min), estimation of ventilation volume, regularity of ventilation, estimation of swimming activity, "digging" or escape activity, and feeding behavior. Ventilation rate was measured; other parameters were ranked.

In Experiments 1 and 2, two flounder were taken daily from each tank (exposed and control) for autopsy, chemical analysis, and histology. In Experiment 3, all flounder were autopsied at the end of a 3-week exposure. All fish were weighed, measured and dissected. Macroscopic examinations of all organs were made and the ovaries, testes, liver and gall bladder were removed. Gonads were weighed, measured and examined microscopically to determine general maturation stage, presence of opaque dead or necrotic eggs, and the gross appearance (color and deliquescense). Maximum egg diameters of 10 eggs from the ovary of each female were measured. Spermatozoa from ripe males were examined under the microscope for motility.

The ventral gonad, gall bladder and half of the liver were placed in clean, preweighed glass culture tubes or glass sample jars. The tubes were sealed tightly with teflon-lined screw caps, the bottles with foil-lined caps. All samples were frozen until they could be analyzed. The dorsal gonad and other half of the liver were preserved in 10% formalin in 1% calcium chloride for histological preparation.

Analytical Procedures:

Analysis of Water Samples. Water samples taken daily from exposure tanks were analyzed for monocyclic aromatic hydrocarbons by extracting one liter twice with 10 ml of TF-Freon and injecting 3.2 microliters of each extract into the gas chromatograph (column packed with 5% SP-1200 and 5% Bentone 34 on 100/120 supelcoport). Liter samples taken daily from solubilizer effluent flowing into the exposure tanks were extracted 3 times with 10 ml of TF-Freon and extracts were injected into the GC. The limit of detectability for monocyclics in water was 0.010 mg/L. In addition, one-liter solubilizer samples were extracted with 80 ml methylene chloride for analysis of dicyclic aromatic compounds.

Extracts were concentrated to about 10 ml and stored in a freezer. Subsequent preparation for analysis followed procedures of MacLeod et al. 1977 and were analyzed on a 10-foot column packed with 5% SP-2100, 1% BMOT on 100/120 supelcoport.

Alkyl cyclohexanes and dicyclics were undetectable in tank water column samples. For results reported here, the concentration was estimated from the concentration in solubilizer effluent and by calculating final tank concentration with the dilution factor.

Analysis of Tissue Samples. Samples analyzed for dicyclic aromatic hydrocarbons and aliphatic compounds were processed according to MacLeod et al. 1977. Samples were analyzed for monocyclic aromatic and alkyl cyclohexane hydrocarbons using procedures developed by project personnel for these experiments (Table 3). In some samples, insufficient weight of tissue (particularly immature gonads) was available, and samples were pooled. In instances where sample weights were below the optimum 10 g, tissue concentrations may be underestimated, particularly of less abundant components. Also, a few liver sample extracts were emulsified and could not be analyzed.

Additional Chemical Analyses. The National Analytical Facility, Seattle, Washington, performed a number of analyses of water, tissue, and crude oil samples by capillary column gas chromatography or mass spectrometry to verify results obtained by in-house analysis and to identify unknown hydrocarbons in tissue and water extracts.

Histological Technique:

Ovaries preserved in 10% formalin in 1% calcium chloride were prepared especially for examination of the lipid distribution in the eggs following the recommendation of Bucke (1972) and using the procedure in Humason (1972). Frozen sections (16 μ) were cut with a cryostat, because routine processing methods would remove lipids. Sections were stained with an oil soluble dye, Oil Red O, counterstained with Harris' Hematoxylin and blued in Scott solution. Staining times were adjusted according to the maturation stages, which varied in stain affinities. One series of sections from each sample was stained with Oil Red O only, another series with Oil Red O and hematoxylin.

Livers were embedded in paraffin and 10 μ transverse and longitudinal sections made. Sections were stained with hematoxylin and eosin according to the procedure in Humason (1972).

Histological Examination:

Each slide was first examined under a low-power (4X or 10X objective) phase contrast microscope and searched for the presence of dead or abnormal eggs. One hundred eggs were counted and closely examined and the percentage dead or abnormal determined. The maximum diameter of the five largest eggs was measured, and the maturation stages ascertained after a complete assessment of all cytological structures occurring at that stage. The maturation stages determined by Yamamoto (1956) for eggs of the flounder, Liopsetta obscura, were found applicable and used in this analysis (11 stages in all). Photomicrographs were taken of control and exposed eggs.

Spawning Induction:

In Experiment 3, an attempt was made to induce the flounder to spawn. Most flounder were adults, but they appeared to be in a post-spawning refractory stage. The technique of Smigielski (1975 a, 1975 b) using carp pituitary (5 mg/454 g total wet weight) in physiological saline solution was employed. Fish were marked with colored thread through the caudal fins so behavior of individual fish could be observed. It was not possible to distinguish sexes in the species with certainty, thus 8 fish were selected at random and injected with carp pituitary, 8 fish were not. The experimental design was as follows:

	Control		Exposed	
	Injected	Not Injected	Injected	Not Injected
Exposed immediately after first injection	2	2	2	2
Exposed 1 week after first injection	2	2	2	2

RESULTS

Morphometrics:

Fish in all experiments were in similar condition. However, more fish in the second experiment were maturing and few females in the third experiment were maturing (Table 1). There were no significant differences between condition for exposed and control fish or length-weight ratios of gonads in the experiments.

The "eyedness" of the flounders was recorded because this genetic feature varies in frequency between populations and with age. For the sample in Experiments 1 and 3, there were approximately 50% right-eyed to 50% left-eyed flounders (Table 1), but more large fish were right-eyed than left-eyed. The differential survival of right-eyed flounder is thought to indicate a physiologically hardier type (Orcutt 1950). In Experiment 3, a higher proportion of the sample was left-eyed; there were more small males in this sample.

Concentrations of Petroleum Components in Test Tanks:

Mean concentrations of petroleum hydrocarbons (WSF) ranged from 115 to 221 μg/L (ppb) in the three experiments (Table 2). Individual component concentrations are given in the Appendix (Table A). Only monocyclic aromatic hydrocarbons were detectable in test tanks, although traces of alkyl cyclohexanes were seen in some samples (Appendix, Table E).

Mortality - Adults:

No mortality occurred at the low exposure concentrations, as expected. In other experiments with flounder, exposed with similar apparatus, mortality was observed at concentrations as low as 1.0 mg/L (ppm) (Yocom et al., manuscript in preparation).

Behavior:

Several behaviors were observed and measured. Usually, individual variation obscures significant treatment differences. In all experiments, however, there was an initial elevation of ventilation rate in exposed fish over that in controls for periods of 2 to 4 days. Eventually, rates of exposed fish dropped and the ventilation rates of exposed and controls were similar. In Experiment 3, the mean ventilation rate of exposed flounder was 45.1 beats/min after the first week and that of controls was 35.7 beats/min. Irregular ventilation rates were also observed in exposed and not in control fish.

Concentrations of Petroleum Components in Tissues:

Tissue concentrations and accumulations of components in ovaries, testes, livers and gall bladders are given in the Appendix (Tables A-E). Means and ranges of monocyclics, alkyl cyclohexanes and dicyclic components are also summarized in Table 4. In Table 4, monocyclics are grouped into monocyclics 1 (M-1) and monocyclics 2 (M-2). The first group (M-1) includes the lowest-boiling-point monocyclics:

benzene, toluene, ethylbenzene, p-xylene, m-xylene and o-xylene. The more substituted monocyclics (M-2) included isopropyl benzene, n-propyl benzene, total C_3-benzenes, total C_4-, and total C_5-benzenes. Alkyl cyclohexanes (CH) identified include methyl cyclohexane, cis 1, 3 dimethyl cyclohexane, 1, 2 dimethyl cyclohexane and a C_3 cyclohexane. Three other unidentified components are probably also C_2 and C_3 cyclohexanes. Dicyclics indentified (D) include naphthalene, 2-methyl naphthalene, 1-methyl naphthalene, and total C_2 naphthalenes.

Monocyclics 2 (M-2) and dicyclics were analyzed only in mature ovaries in Experiment 2. All monocyclics, cyclohexanes, and dicyclics were analyzed in tissues of Experiment 3. Since fewer maturing ovaries occurred in Experiment 1, not all of these samples were analyzed. Monocyclic concentrations in maturing ovaries were similar to those in Experiment 2. Other experiments (Yocom et al, manuscript in preparation) indicated no detectable levels of any components in 120 tissue samples from control flounders. Therefore, only a few controls were analyzed in these experiments. No components were detected in any controls.

Ovaries. Immature ovaries accumulated much lower concentrations of monocyclics and alkyl cyclohexanes (mean total - 0.890 μg/g; Table 4) than mature ovaries (mean total = 8.585 μg/g monocyclics and alkyl cyclohexanes; 12.976 μg/g all monocyclics, cyclohexanes, and dicyclics; Table 4). Uptake of components was rapid, near maximum concentrations occurring after 24 hours of exposure (Figure 2). The maximum accumulation of components in any ovary was 14.618 μg/g.

Proportions of the components remained relatively constant throughout the experiment (Figure 2). The accumulation of alkyl cyclohexanes was of some interest, since these components have not previously been identified as biologically active components of crude oil and yet appear in relatively high concentrations in both ovarian and liver tissues (Yocom et al, manuscript in preparation-b). A gas chromatogram of the freon extract of adult starry flounder ovary exposed for approximately 7 days (Exp. 2) is shown in Figure 3; individual monocyclic and alkyl cyclohexane components are labeled.

The maximum accumulations over water column concentrations are given in the Appendix (Tables A-E), and are summarized in Table 4 and Table 5 (ovaries only). The maximum accumulation was determined by dividing the tissue concentration by the water concentration. In the case of components not detected in tank water samples (monocyclics and alkyl cyclohexanes < 0.010 mg/g; dicyclics < 0.00025 mg/g) the tank concentrations were estimated (see Methods).

Maximum accumulation of all monocyclics, alkyl cyclohexanes, and dicyclics in mature ovaries was approximately 80 to 200X (mean = 112.8X) and of monocyclics (M-1 only) and cyclohexanes was approximately 50 to 160X (mean = 74.6X) the water concentration (Tables 4 and 6). In immature ovaries, the maximum accumulation of monocyclics (M-1 only) and and alkyl cyclohexanes was approximately 3 to 10X (mean = 7.7X) the water concentration.

Testes. There were no immature males in the samples. Testes of mature males accumulated no detectable levels of components after 1 week of exposure (Table 4). However, after 3 weeks of exposure (Appendix, Table D) 0.313 to 1.361 µg/g of toluene accumulated in the testes. No other component was detectable. Uptake in the testes was low and much slower than in ovaries. The maximum accumulation of toluene after 3 weeks of exposure was approximately 3X to 6X the water concentration.

Livers. The concentrations of monocyclics (M-1 only) and alkyl cyclohexanes were determined after 1 week of exposure for livers of both males and females (Table 4). Mean concentrations of these components were 8.450 µg/g in mature males, 15.535 µg/g in mature females, and only 1.346 µg/g in immature females. Data over the 1-week test period indicate an increasing concentration with time, thus uptake does not reach a maximum level rapidly as in the case of the gonads. After 1 week of exposure mean maximum accumulations in mature adults were approximately 70X (males) and 135X (females) the water concentration (Appendix, Tables A-C). After 3 weeks of exposure, maximum monocyclic accumulations were approximately 200X to 400X (immature females) and 225X to 290X (mature males) the water concentration (Appendix, Table D). Maximum accumulation of cyclohexanes was approximately 2600 to 8750X the water concentration (Appendix, Tables B and E).

Gall Bladders. The weight of tissue available for component analysis in gall bladders containing bile was insufficient in most cases, but analysis of monocyclics and cyclohexanes in gall bladders of fish in Experiment 2 (Appendix, Table A) showed that the concentration was approximately the same in gall bladders of males and females and did not significantly increase throughout the 7-day exposure period (0.280-0.469 µg/g). Only toluene was present, no other monocyclics or cyclohexanes were detected. The maximum accumulation in gall bladders was approximately 2 to 4X the water concentration of toluene.

All Tissues. Among the six monocyclics (M-1), the relative accumulation of toluene was the highest, generally followed by m-xylene, benzene, o-xylene, ethylbenzene and p-xylene, respectively. Of the cyclohexanes (CH), methyl cyclohexane reached highest concentrations, followed by cis 1, 3 dimethyl cyclohexane, and 1, 2 dimethyl cyclohexane. Among the more substituted monocyclics (M-2) the highest concentrations were of the C_3-benzenes, followed by C_4-benzenes and C_5-benzenes, respectively. And finally, among the dicyclics (D), naphthalene was highest in concentration followed by 2-methylnaphthalene and 1-methylnaphthalene, respectively. These general proportions were approximately the same in liver tissues of both sexes. In mature ovaries, however, the relative abundance of monocyclics was slightly different than in livers, the concentration of benzene being higher than m-xylene.

Autopsies:

Liver. Some exposed fish showed gross effects in the appearance of the liver. After a few days of exposure, livers appeared to have hemorrhagic areas and were mottled.

There was considerable variation in liver color, from bright yellow to dark red (Table 1). There was no obvious correlation with sex, size or exposure to WSF. There is an indication that the color variation is associated with gonadal maturation, with fewer fish having yellow livers at later maturation stages (Table 1).

Ovaries. Exposed fish showed some effects in the appearance of the ovary. Exposed ovaries were paler yellow than controls of equivalent maturation stage. These ovaries also contained some opaque white eggs, visible on the surface, appearing to be necrotic foci with several dead eggs when examined microscopically. The capillary network over the ovarian membrane of exposed fish contained blood, but the network appeared paler red than in controls. Microscopic examination indicated hemolysis of red blood cells had occurred, lending to the overall paler appearance of exposed ovaries. There were dead eggs seen in most of the maturing ovaries (Table 6). Dead eggs were not obvious in immature ovaries. Because the differences between control and exposed fish were subtle, further comparison was made histologically (see below).

Testes. No obvious differences were noted in the appearance of the testes. No difference in spermatozoan motility between control and exposed males was measured.

Histological Effects on Eggs:

Abnormalities and Mortality. Abnormal and dead eggs were first observed in immature and maturing ovaries of exposed females by day 2 of the exposure (Table 5, Table 6). These abnormal and dead eggs were observed throughout the remainder of the experiment. Ovaries of fish examined 1 week after the cessation of exposure and depuration had the most dead and abnormal eggs, indicating that effects were not reversible.

The mean percentages of abnormal eggs in exposed were 13.2% in immature and 3.0% in mature females of Exp. 1 and 0.5% in immature and 13.0% in mature females of Exp. 2. The mean percentages of dead eggs were 5.5% in immature and 5.8% in mature females of Exp. 1 and 0.2% in immature and 15.0% in mature females of Exp. 2 (Table 7).

The commonest abnormality observed in both immature and mature eggs was the occurrence of clear vacuoles extruding through the cytoplasm of the egg, usually near the periphery (Figs. 4B, 5B, 6B). The vacuoles were colorless with oil red O staining, indicating that they are not lipid deposits. These vacuoles were never observed in control eggs (Figs. 4A, 5A).

Dead eggs in immature ovaries occurred in necrotic foci, and appeared to be atresic (Figs. 7B, 8A, 8B). By the end of the exposure period, and particularly after the subsequent depuration period, reduced numbers of eggs appeared to occur in exposed immature ovaries compared to controls (Figs. 7A and B), possibly indicating resorption. The first change appeared to be coalescence of nucleoplasm into fewer droplets (Fig. 8A) until only one droplet was present, the nuclear membrane still intact. The coalesced droplet had a different staining affinity, appearing purple rather than blue as do nucleoli of controls and unaffected exposed eggs. Subsequently, the nuclear membrane disappeared, the droplet remaining, with simultaneous necrosis of the cytoplasm and disintegration of the cell membrane (Fig. 8B).

Dead maturing eggs also occurred in necrotic foci (Fig. 9B). The eggs were disintegrating and appeared to have thicker cell membranes (zona radiata) than the intact controls (Fig. 9A). With red oil O staining, yolk globules appeared a darker red-brown color than the normal red-pink globules of control eggs. Although present in exposed ovaries, the foci of dying and dead mature eggs were difficult to detect histologically with only a few sections from each ovary.

Acceleration of Maturation:

Females. Another apparent effect is the acceleration of egg maturation in exposed flounder over that in controls (Table 7). The stages of Yamamoto (1956; 1-11) were used to assess maturation so that differences between controls and exposed attributable to different maturation stages would not be confused with the effects of exposure. A complete description of egg maturation in starry flounder will be published separately (Bowers and Whipple, manuscript in preparation).

In Experiment 1 (January; Table 5) immature ovaries contained eggs in stages 1 to 3 (1 = chromatin-nucleolus, 2 = early perinucleolus, and 3 = middle to late perinucleolus). Maturing ovaries were in stages 4 and 5 (yolk = yolk vesicle, and 5 = primary yolk stage). In Experiment 2 (February; Table 6) immature ovaries were in stages similar to those in Experiment 1 (stages 1 to 3). In maturing ovaries, however, control eggs were predominantly in stage 6, or 6 to 7 (6 = secondary yolk stage, 7 = tertiary yolk stage). None had reached the full tertiary yolk stage (7). Among the exposed, several ovaries showed eggs in later stages 7 and 8 (7 = tertiary yolk stage and 8 = migratory nucleus stage). Maturing flounder contain eggs in two stages, having eggs in perinucleolus stages as well as the predominant maturation stage.

Table 7 summarizes the means of several parameters showing acceleration of maturation in ovaries of exposed flounder for Experiment 2. An indication of acceleration of maturation in females of Experiment 1 was also noted. Table 7 shows that ovaries of exposed maturing females not only had a higher frequency of more advanced maturation stages, but also that the mean maximum egg diameter was greater. These observations correlate with the higher gonadosomatic index (GSI) in exposed (6.59) than in control (5.64) females. Since the GSI is based on the ratio of ovary weight to body weight and because relatively small females contained advanced maturation stages, the indication is that acceleration in maturation was due to exposure and not a function of the size of the female.

Males. Histological sections of testes were not made. However, the GSI of males also indicated an acceleration of maturation due to exposure. Sample sizes of males in Experiments 1 and 2 were too small. However, the males in Experiment 3 (exposed for 3 weeks) had a higher mean GSI (0.387; n=5) than did controls (0.140; n=7). Further, 80% of the exposed males were ripe, while only 29% of the controls were ripe.

Histological Examination of Livers:

Examination of liver tissue showed that, after 5 to 7 days exposure to 115 ppb WSF, livers were highly vacuolated and the hepatic muralia were disorganized in both male and female flounders (Figs. 10B, 11B). Cytoplasmic vacuolization increased with exposure time. Similar effects were also seen in livers of flounder allowed to depurate for 1 week after the 1 week exposure period, indicating the effects may not be reversible, as the degree of vacuolization was greater. Sloughing of endothelial tissue in blood vessels was found in livers of some exposed flounder. These changes were not seen in livers of control flounder (Figs. 10A, 11A).

CONCLUSIONS AND DISCUSSION

Starry flounder exposed to approximately 100 ppb of the WSF of Cook Inlet crude oil exhibited several effects, including elevated activity and ventilation (respiration), erythrocyte destruction, abnormalities and necrosis in eggs and liver tissue, and acceleration of maturation in both males and females (Table 8).

Flounder were exposed only to WSF components in the water column. In the field, exposure could occur from two other routes; sediments and food. The exposure concentrations in these experiments (approx. 100-200 ppb) are probably higher than in the field. Although measurements of aromatics in natural waters are scarce, available field data show that chronic concentrations of total aromatics in water may reach levels of 1-30 ppb offshore (Clarke et al. 1977b; Hiltabrand 1978). Concentrations are probably higher in polluted estuaries. In addition, an exposure of 7 days is less than flounder would experience in a chronic field situation. Sediment concentrations of aromatic hydrocarbons (Clarke et al. 1977b) reach levels of approximately 1,000-60,000 ppb (wet wt.). Flounder would also be exposed to aromatics in sediments in chronically polluted areas. Field measurements of alkyl cyclohexanes in water or sediments are not available. Flounder could also be exposed to WSF components of petroleum through contaminated food. However, in later prespawning maturation stages, flounder do not feed (Orcutt 1950) and other experiments at our laboratory (Yocom et al., manuscript in preparation) show that when nonspawning adults were fed contaminated littleneck clams (8.0 μg/g M-1+CH), they accumulated 1.72 μg/g in their livers (CH only) compared to flounder exposed through the water column (0.100 mg/L M-1+CH) and fed uncontaminated clams, which accumulated 180.8 μg/g (M-1+CH). Lack of accumulation of the toxic aromatic fraction from food may partially explain the relatively few effects observed in rainbow trout exposed prior to reproduction to petroleum in their diet, as observed by Hodgins et al. (1977a). The major route of accumulation of the more toxic aromatics would appear to be through water column and sediment exposures. The exposure concentration in our experiments is probably a reasonable approximation to chronic exposure of flounder in the field.

No flounders died in these experiments, but behavior was affected. There was an elevation in activity and ventilation, indicating an increased respiration and metabolic rate. A return to control levels occurred subsequently. Similar results were obtained in other studies of larvae and adults of salmon, striped bass, and Pacific herring exposed to sublethal levels of benzene (Brocksen and Bailey 1973; Eldridge et al. 1977) and in other fish and invertebrates exposed to sublethal levels of WSF of crude and refined oil (Anderson et al. 1974a). The behavior of adult herring prior to spawning was greatly affected by exposure to ppb levels of benzene, including rapid ventilation, disequilibrium, and premature spawning (Struhsaker 1977).

Uptake and total accumulation of monocyclics (M-1) and alkyl cyclohexanes (CH) in gonads and livers of flounder varied with sex and maturity (Table 8). Highest mean accumulation occurred in livers of adult females with gonads in the resting stage (2800X; Yocom et al., manuscript in preparation) and lowest in immature females (12X). Mature males accumulated 74X and mature females 135X the concentration of M-1 and CH in the water. Concentrations increased with time in livers of all flounders, reaching much higher levels after 3 weeks than after 1 week of exposure.

Uptake and accumulation of M-1 and CH in gonads also varied with sex and maturity. Rate of uptake was much faster in mature ovaries than in livers, with maximum concentrations in about 24-48 hrs. Concentration levels of all components measured (M-1, CH, M-2, D) remained at an equilibrium level for the remainder of the exposure period. Maximum accumulation was highest in female ovaries (75X), lowest in male testes (not detectable). Ovaries of immature females and resting ovaries of mature females accumulated comparatively low concentrations (7X, 8X respectively).

Variation in accumulation in the liver may be related to feeding and resultant metabolic rates. Adult flounders in the resting stage were fed clams and probably had a faster rate of metabolism and uptake than did sexually maturing male and female flounders and immature females which were not fed. The variation in accumulation of lipid-soluble components in gonads is probably a function of the amount of lipid; maturing ovaries containing far more lipid than immature ovaries and testes containing even less lipid.

Although tissue samples are available for analysis of alkanes, we have not completed these analyses. Anderson (1974a) suggested that although alkanes and aromatic hydrocarbons are both accumulated, the aromatics are concentrated to higher levels and retained longer than the alkanes. Kühnhold et al. (see paper in this proceedings) found that winter flounder accumulated relatively low concentrations of alkanes from low ppb levels of No. 2 fuel oil after long exposures while accumulating higher levels of aromatics. Alkanes are believed to be less toxic than aromatics, although more recent work suggests they may have narcotic effects and cytotoxicity (Clarke et al. 1977a).

The highest total concentrations in ovaries were of M-1, followed by CH, M-2 and D. The proportions of M-1, CH, M-2 and D remained fairly constant in mature ovaries over the exposure period. In livers, however, the relative proportions of M-1 and CH changed, with cyclohexanes increasing relative to monocyclics with time. Concentrations of individual components in mature ovaries after 7 days of exposure were as follows, in decreasing order: methyl cyclohexane, toluene, benzene, C_2 cyclohexane (unidentified #1), m-xylene, Cis 1, 3 dimethyl cyclohexane, ethylbenzene, 1, 2 dimethyl cyclohexane, C_3 cyclohexane, o-xylene, C_3 cyclohexane (unidentified #3) and p-xylene. Mean total accumulation of alkyl cyclohexanes after 7 days of exposure was much higher than of monocyclics-1 (890X, 68X water concentration, respectively). The high accumulation of cyclohexanes in ovaries and livers from undetectable levels in water is of interest since they have not been previously identified as biologically active components. The toxicity of the cyclohexanes is not well known. Some data indicate that they are as toxic to fish as are monocyclic aromatics (Pickering and Henderson 1966), but information is so incomplete that no definite statement can be made. The mean total accumulation of M-2 and D in ovaries after 7 days of exposure was approximately 260X water concentration. Highest concentrations of individual M-2 and D components in mature ovaries were of methylated naphthalenes.

When the relative concentrations of components in both liver and gonadal tissues are compared to concentrations in the water, it is apparent that differential uptake has occurred. Many components are undetectable in the water column but accumulate to very high levels in the liver and gonads, particularly the alkyl cyclohexanes.

A recent review by Clarke et al. (1977b) shows that few laboratory experiments have been done on the accumulation of toxic WSF components in ovaries or testes of fish. Work by Zitko (1971) on the flounder, Pseudopleuronectes americanus, showed a total aromatic concentration of 622 μg/g wet weight in the "guts" of flounder exposed to Bunker C. Previous work at the Tiburon Laboratory, with herring exposed to 100 ppb benzene prior to spawning, showed a concentration of 1.2 μg/g wet weight benzene in mature ovaries after a 48-hr exposure. This is comparable to the uptake of benzene in mature ovaries of flounder (1.27 μg/g) after 48 hrs. In addition, few laboratory experiments measuring accumulation of monocyclics in specific tissues have been made. Korn et al. (1976-1977) measured uptake of radioactive labeled benzene in several tissues (not mature ovaries) of northern anchovy, striped bass and Pacific herring. Residues of benzene and toluene in liver tissue of herring are comparable to those measured here in flounder, with toluene reaching higher concentrations than benzene. Clarke et al. (1977b) summarizes a few other laboratory studies on uptake in fish and tissue levels of other aromatics.

In the review by Clarke et al. (1977b), tissue levels of aromatics measured in field-captured fishes show that from 0.4 to 22 μg/g wet weight occurred in whole tissue. Zitko (1971) measured 21 μg/g aromatics in the "guts" of field specimens of P. americanus exposed to Bunker C. These data indicate that tissue levels of aromatics in field-captured flounder correspond to those measured in starry flounder exposed to 100 ppb of the WSF of crude oil in this study (liver = 1-20 μg/g in 7 days), and that comparable deleterious effects may also occur.

The effects of exposure are summarized in Table 8. Most effects are similar to those described by Couch (1975), Walsh and Ribelin (1975) and Smith and Cole (1973) for pesticide exposures and are probably generalized sublethal responses of fish to hydrocarbon exposure.

Some effects on the liver, such as disruption of the organization of hepatic muralia and increased lipid deposition could have been accentuated by the 7-day exposure period when flounder were not fed. However, these effects were not observed in control livers. Further, maturing fish normally do not feed. Starvation stress may have interacted with the petroleum stress to produce the pronounced effects on livers of immature fish. Similar tissue effects were observed in livers of English sole exposed to oiled sediments (McCain et al. 1978) and of rainbow trout exposed to oil in food (Hodgins et al. 1977a). Other histopathological effects of oil were reviewed by Hodgins et al. (1977b).

The WSF of Cook Inlet crude oil resulted in both direct and indirect effects on starry flounder in the various maturation stages (Table 8) (see also Kühnhold et al., this proceedings). There were direct effects on eggs (necrosis and abnormalities) which may have indirectly reduced subsequent fertilization, hatching, larval growth and survival. There also appeared to be an indirect effect on hormones promoting gametogenesis, with maturation accelerated in exposed flounder.

There seemed to be no effect of exposure on testes or sperm motility in mature males. However, tissue sections of testes were not made, and subsequent work may reveal effects on a cellular level. Numerous changes in eggs from exposed fish at all stages were noted, including egg death. In immature eggs, the apparent death or disintegration of eggs may have been due to atresia or resorption. A few atresic eggs were observed in control immature females also, although the effect was more pronounced in exposed immature females. As in the liver, atresic eggs in immature females may result from interaction of starvation stress with petroleum stress. Egg abnormalities consisted largely of vacuolization; never observed in eggs from controls. The vacuoles may result from an effect of petroleum hydrocarbons on osmoregulation and the hydration of ovaries.

Maturation was accelerated in exposed flounders (Table 8). Exposed males had higher gonadosomatic indices and a higher percentage of testes undergoing spermiation. Exposed females contained eggs in later maturation stages than control eggs, with increased vitellinogenesis (yolk globules = vitellin = phosolipids; Yamamoto, 1957) and larger egg size. The gonadosomatic indices of exposed females were also higher than controls. An explanation of the acceleration in maturation involves the observation that detoxification of petroleum hydrocarbons requires enzymes of the mixed-function-oxidase (MFO) system which also hydroxylate steroids and are involved in pre-oxidation of lipids. The MFO enzymes, bound to the ribosomes, function in several biochemical pathways of organisms. 17-α-hydroxyprogesterone is the major hormone inducing maturation of eggs in female winter flounder (Campbell et al. 1976) and normally undergoes hydroxylation to adrenocortical steroids in the MFO system. If aromatic and cyclohexane components competitively inhibit this function, they may potentiate the effect of progesterone thus accelerating egg maturation. Simultaneously the oil components may inhibit the pre-oxidation of lipids and the formation of adrenocortical steroids, affecting water balance and lipid deposition. Similar competitive inhibition of toxicants occurs in mammals (LaDu et al. 1972; Doggett et al. 1977) and may also function in fish exposed to petroleum (Brocksen and Bailey 1973).

The tissue-level effects seen at the end of the exposure period were also present after 7 days of depuration, and appear to be irreversible. The results of Kühnhold et al. (see paper, this proceedings) also indicate that this does occur, with reductions in survival and growth of later stages. A 50% reduction in fecundity, and larval survival through hatching and yolk absorption, was also observed in herring exposed to low ppb benzene prior to spawning (Struhsaker 1977).

A number of studies of the effects of petroleum have shown an initial stimulation of several parameters when organisms are exposed to low sublethal levels, while at higher acute levels a depression or narcosis occurs (Brocksen and Bailey 1973; Anderson 1974a; Eldridge 1978). This phenomenon was described by Smyth (1967) as a sufficient challenge. An example cited was increased growth at low exposure levels of pesticides. However, stimulation by toxicants may not be ultimately beneficial to the organism, as demonstrated here. Also, with chronic exposures, the ability of the organisms to homeostatically adjust may collapse or there may be an energy depletion resulting in decreased growth or reproduction.

The cause-and-effect relationships between the components of crude oil measured in these tissues and the physiological or histological effects observed cannot be ascertained definitely. It is difficult to demonstrate which components or interacting components are exerting the primary effects. That a single component can produce similar effects in herring has been discussed previously (e.g. benzene, Struhsaker 1977). Finally, it is not clear whether the toxic effects are caused by the unchanged components or their metabolites, as pointed out by Malins (1977).

In conclusion, the preliminary results of these experiments indicate strongly that low levels of the WSF of crude oil, approximating chronic exposures, can result in deleterious effects that reduce the fecundity of flounder. The total reduction in survival through spawning, hatching and larval stages cannot be assessed, but results indicate a probable reduction in viable eggs of approximately 15-30%, assuming abnormal eggs will not survive. In herring, the reduction in survival through yolk absorption was estimated as 50% (Struhsaker 1977). These effects occur at concentrations two orders of magnitude less than the acute 96-hr TLMs. Further, if exposure to oil stimulates gametogenesis and spawning, spawning fish may be induced to release eggs in areas of high petroleum concentrations (e.g. oil spill), thus exposing relatively sensitive stages to the effects of the oil.

Although sublethal effects of petroleum on individual organisms in small subsamples have been demonstrated readily in laboratory studies, evidence for these effects occurring in organisms in the field on a population level has been more difficult to provide. Natural variation in population sizes of most species often obscures variation due to a pollutant. Few "fish kills" have been irrefutably linked with a specific pollutant or spill event, particularly in estuarine situations. We suspect, however, that slow population declines of several estuarine-dependent species may be at least in part due to the interaction of chronic pollution with normal environmental stress, such as occurs during spawning. A gradual decline in production of the population may take the form of reduced growth or in the inhibition of reproduction. The latter may occur if spawning years are missed, egg production is reduced, and egg viability decreased. An assessment of the reduction in survival of gonadal eggs by exposing fish in the laboratory prior to spawning enables us to obtain a more direct estimate of the potential reduction in year-class survival attributable to a particular pollutant.

If marine organisms prove generally to be more sensitive during their spawning season, fishery management decisions should consider timing of oil-related activities to adequately protect fishery resources.

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Table 1. Morphometrics of starry flounder subsamples. Experiments 1, 2, 3.

Exp. No. Date	Tot. No.	Fem. No. (%)	Male No. (%)	Sex Ratio (♀:♂)	Eye*		Females**		Ovaries			Maturing Females (%)
					L (%)	R (%)	SL (cm)	WW (g)	TL (cm)	W (cm)	WW (g)	
1 1/19	30	19 (63)	11 (37)	2:1	50	50	39.3 (32.9-50.0)	1140 (652-1877)	10.4 (6.0-18.5)	4.6 (2.0-9.2)	24.20 (2.64-113.30)	32
2 2/12	40	28 (70)	12 (30)	2:1	45	55	35.6 (29.2-41.3)	1042 (549-1707)	13.0 (2.4-23.0)	5.6 (1.9-11.0)	48.8 (1.58-153.00)	67
3 4/25	16	4 (25)	16 (75)	1:3	87	13	35.0 (30.5-38.0)	1172 (710-1360)	7.9 (1.2-16.0)	3.1 (1.0-6.0)	15.7 (0.56-51.22)	25

Exp. No. Date	Liver Color--Both Sexes		Males**		Testes			Ripe Males (%)
	Yellow (%)	Red (%)	SL (cm)	WW (g)	L (cm)	W (cm)	WW (g)	
1 1/19	76	24	37.1 (32.1-44.1)	911 (686-1300)	4.0 (1.2-10.0)	1.5 (0.5-3.5)	2.54 (0.13-7.50)	38
2 2/12	67	33	32.4 (29.8-35.4)	707 (586-872)	4.5 (2.5-6.0)	2.0 (1.0-3.0)	4.03 (0.28-6.12)	75
3 4/25	100	0	32.9 (29.5-37.2)	915 (540-1270)	3.7 (1.7-6.5)	1.4 (0.5-2.0)	1.93 (0.14-6.53)	58

*Side of fish with most dorsad eye and the dorsal operculum; R = right, L = left.
**Values in parentheses are ranges; other values are means for that experiment.

SL = Standard Length; WW = Wet Weight; TL = Total Length.

Table 2. Experimental conditions. Starry flounder exposed during egg maturation prior to spawning (Experiments 1, 2) and after spawning (Experiment 3). Values in parentheses are ranges, other values are means.

Exp. No.	Dates Days Hrs.	Treatment	Fish			Mean Water* Concentration (mg/L (ppm)	Oxygen (ppm)	Temperature (°C)	Salinity (ppt)	Volume Water (Liters)	Flow Rate (L/Min)
			No.	Tot. WW (Kg)	WW/L (g)						
1	1/18 to 1/23 5 120	Control	15	14.70	16.97	0	6.1 (5.0-8.6)	10.7 (9.5-11.7)	19.7 (19.0-21.0)	866	3 (1-3**)
		Exposed	15	17.57	20.29	0.140 (.041-.326)	5.8 (4.6-8.0)	Same	Same	Same	Same
2	2/12 to 2/19 7 168	Control	20	19.02	21.96	0	8.2 (7.0-8.7)	13.7 (12.5-14.5)	29.1 (29.0-30.0)	866	7 (3-7**)
		Exposed***	20	20.35	23.50	0.115 (0.45-.353)	7.9 (6.4-8.8)	Same	Same	Same	Same
3	4/25 to 5/15 21 504	Control	8	7.15	8.25	0	7.7 (6.1-8.8)	17.2 (15.8-18.5)	18.8 (16.5-19.5)	866	8
		Exposed	8	8.52	9.84	0.221 (.144-.265)	7.7 (6.4-8.6)	17.4 (15.9-18.8)	Same	Same	Same

*Water Concentration = total of 6 monocyclic aromatics in WSF (M-1); benzene, toluene, o-, m-, p-xylene, ethylbenzene. Cyclohexanes (CH), other monocyclics (M-2) and dicyclics (D) undetectable in water samples (<0.010 mg/L).

**Flow rate was too low; increased during first exposure day.

***Remaining fish fed after exposure for 1-wk depuration period.

WW = Wet Weight

Table 3. Procedure for analysis of low-boiling-point hydrocarbons in animal tissues. (Benville et al, MS in prep.)

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1. Place 10 grams of tissue in a clean, glass culture tube (with a teflon-seal screw cap).
2. Add 6 ml of 4N NaOH and 4 ml of TF-Freon and cap tightly.
3. Place tube in oven (or water bath) for 18 hours at 30°C. Shake tube 4 or 5 times during this time.
4. Remove tube from oven and shake vigorously for one minute.
5. Centrifuge tube (while still warm) for 10 minutes at 3000 rpm.
6. If freon layer is clear (not cloudy), draw off with pipette and store in a clean, glass vial with a teflon-seal screw cap until ready to inject on GC.

Emulsions:

If the freon layer is clouded, use following procedure:

7. Freeze clouded sample and recentrifuge while still frozen (20-30 minutes at 2000-3000 rpm).
8. If sample is still cloudy, repeat.
9. If sample has not cleared, add 1-2 ml of 20% H_2SO_4, shake, and recentrifuge. A 15-20% reduction in recovery will result if it is necessary to follow this step.

RECOVERY RATE = 90-96% if tubes remain tightly capped.

LEVEL OF DETECTION = 0.025 μg/g wet weight.

Table 4. Summary of mean concentrations of monocyclic and dicyclic aromatic and cyclohexane components in gonads of immature and maturing starry flounder exposed to the WSF of Cook Inlet crude oil during gonadal maturation. Experiment 2. No immature males in samples. Percentages of total concentrations in parentheses. Tissue concentrations are in μg/g wet weight.
Total Accumulation = Total Mean Tissue Concentration (μg/g)/Mean Water Concentration (0.115 mg/L).

Treatment	Sex	Maturity	Tissue	No.	Mean M-1	Mean CH	Mean M-2	Mean D	Total Mean M-1+CH	Total Mean All	Total Accumulation M-1+CH	Total Accumulation All
Exposed	M	Mature (Ripe)	Testis	5	ND	ND	–	–	ND	–	ND	–
			Liver	4	5.891 (70)	2.559 (30)	–	–	8.450	–	73.5X	–
	F	Im-mature	Ovary	2	0.181 (20)	0.709 (80)	–	–	0.890	–	7.7X	–
			Liver	2	1.346 (100)	ND (0)	–	–	1.346	–	11.7X	–
	F	Mature	Ovary	6	4.801 (37)	3.784 (29)	2.228 (17)	2.163 (17)	(8.585)	12.976	74.6X	112.8X
			Liver	5	9.708 (63)	5.827 (37)	–	–	15.535	–	135.1X	–
Control	F	Im-mature	Ovary	1	ND	ND	–	–	ND	–	0	0
			Liver	1	ND	ND	–	–	ND	–	0	0
	F	Mature	Ovary	2	ND	ND	–	–	ND	–	0	0
			Liver	2	ND	ND	–	–	ND	–	0	0

M-1 = Monocyclics-1 = Benzene, toluene, ethylbenzene, p-xylene, o-xylene, m-xylene.
CH = Cyclohexanes = Methyl cyclohexane, Cis 1, 3 dimethyl cyclohexane, 1, 2 dimethyl cyclohexane, C_3 cyclohexane and 3 unidentified compounds, also probably cyclohexanes.
M-2 = Morocyclics-2 = Isopropyl benzene, n-propyl benzene, total C_3 benzenes, total C_4 benzenes and total C_5 benzenes.
D = Dicyclics = Naphthalene, 2-methyl naphthalene, 1-methyl naphthalene, total C_2-naphthalenes.
*Monocyclics-2 (M-2) and dicyclics (D) measured only in mature ovaries.

Table 5. Summary of results from histological examination of ovaries of adult flounder exposed to the WSF of Cook Inlet crude oil prior to spawning. Experiment 1.

Day Date	Treat-ment	Mean WSF-[illegible] Concen. (mg/L)	Matu-rity[1]	L (cm)	WW (g)	GSI[2]	Mat. Stage (1-11)[3]	Description	[illegible] Diam. (μ)	% Abn.	Dead
0.25 1/19	Cont.	ND	Imm.	8.5	6.2	0.58	3	Perinucleolus	120	0	0
	Exp.	0.118	Imm.	7.0	5.2	0.48	3	Perinucleolus	100	0	0
	Exp.		Imm.	7.0	3.8	0.55	3	Perinucleolus	120	0	0
1 1/20	Cont.	ND	Mat.	12.0	27.7	2.26	4 to 5	Yolk Vesicle to Primary Yolk	130 to 280	0	0
	Exp.	0.090	Mat.	10.0	17.1	1.43	4	Yolk Vesicle	260	0	0
2 1/21	Cont.	ND	Imm.	6.2	4.1	0.42	3	Perinucleolus	100	0	0
	Exp.[4]	0.098	Mat.	18.0	91.9	5.40	6	Secondary Yolk	460	3	[illegible]
3 1/22	Cont.	ND	Mat.	8.0	8.0	0.73	4	Yolk Vesicle	200	0	0
	Exp.	0.224	Mat.	18.5	113.3	6.04	6	Secondary Yolk	410	5	[illegible]
	Exp.		Imm.	5.2	2.6	0.35	3	Perinucleolus	120	21	12
4 1/23	Cont.	ND	Imm.	10.0	6.0	0.62	3	Perinucleolus	100	0	0
	Exp.	0.226	Imm.	7.0	4.4	0.36	3	Perinucleolus	100	32	10
	Exp.		Mat.	14.5	47.2	3.00	4 to 5	Yolk Vesicle to Primary Yolk	150 to 310	4	[illegible]

[1] Mat. Early maturation stages.
Imm. = Not maturing as yet, although adults.

[2] GSI = Gonadosomatic Index = Ovary Wet Weight X 100/Body Wet Weight.

[3] Stages from Yamamoto, 1956.

[4] [illegible] = 6.470 μg/g (wet weight).

Table 6. Summary of results from histological examination of ovaries of adult flounder exposed to the WSF of Cook Inlet crude oil prior to spawning. Experiment 2.

Day Date	Treat-ment	WSF-MA-1 Concen. (mg/L)	Tissue Concentrations (µg/g)[1]						Accumulation		Matu-rity	Ovary			Mat. Stage (1-11)[3]	Description	Mean Max Diam. (µ)	% Abn.	% Dead
			M-1	CH	M-2	D	Total M1+CH	All	M1+CH	All		L (cm)	WW (g)	GSI[2]					
0.25	Cont.	0	ND	ND	-	-	ND	-	ND	-	Imm.	2.8	0.70	0.07	3	Perinucleolus	100	0	0
2/12	Exp.	0.182	0.363	0.187	-	-	0.550	-	3X	-	Imm.	7.0	4.29	0.46	3	Perinucleolus	100	0	0
1	Cont.	0	ND	ND	ND	ND	ND	ND	0	0	Mat.	21.2	110.0	7.62	6	Secondary Yolk	560	0	0
2/13	Exp.	0.123	4.652	3.646	-	-	8.298	-	67X	-	Mat.	19.0	99.0	7.26	7	Tertiary Yolk	670	0	0
	Exp.	0.123	3.506	2.996	1.977	1.903	6.502	10.382	53X	84X	Mat.	12.5	39.5	3.66	6	Secondary Yolk	460	0	0
2	Cont.	0	ND	ND	-	-	ND	-	0	-	Imm.	7.1	3.33	0.35	3	Perinucleolus	120	0	0
2/14	Exp.	0.119	ND	1.232	-	-	1.232	-	10X	-	Imm.	7.0	3.94	0.51	3	Perinucleolus	120	1	10
3	Cont.	0	ND	ND	-	-	ND	-	0	-	Mat.	23.0	129.0	7.66	6	Secondary Yolk	560	0	0
2/15	Cont.	0	ND	ND	-	-	ND	-	0	-	Mat.	22.0	97.0	8.52	6	Secondary Yolk	560	0	0
	Exp.	0.088	4.877	3.048	2.277	2.138	7.925	12.340	90X	140X	Mat.	20.0	150.0	8.79	7	Tertiary Yolk	670	15	12
4	Cont.	0	ND	ND	-	-	ND	-	0	-	Imm.	5.5	3.50	0.48	3	Perinucleolus	120	0	0
2/16	Cont.	0	ND	ND	-	-	ND	-	0	-	Mat.	14.5	45.0	3.70	6	Secondary Yolk	460	0	0
	Exp.	0.104	5.720	4.528	2.336	2.034	10.248	14.618	98X	140X	Mat.	18.0	82.0	5.37	6	Secondary Yolk	560	28	20
5	Cont.	0	ND	ND	-	-	ND	-	0	-	Mat.	11.5	43.0	4.20	6	Secondary Yolk	460	0	0
2/17	Exp.	0.112	5.043	3.609	2.390	2.327	8.652	13.369	77X	119X	Mat.	21.5	141.0	10.23	7	Tertiary Yolk	670	20	33
	Exp.	0.112	4.136	3.023	-	-	7.159	-	64X	-	Mat.	14.0	43.0	5.26	6	Secondary Yolk	460	5	8
6	Cont.	0	ND	ND	-	-	ND	-	0	-	Mat.	17.0	80.0	6.58	6	Secondary Yolk	510	0	0
2/18	Cont.	0	ND	ND	-	-	ND	-	0	-	Mat.	13.5	34.0	3.12	6	Secondary Yolk	410	0	2
	Exp.	0.075	11.871	(M-1+CH)	-	-	11.871	-	158X	-	Mat.	17.5	66.0	5.40	6	Secondary Yolk	510	32	25
	Exp.	0.075	4.396	3.606	2.009	2.554	8.002	12.565	107X	167X	Mat.	14.0	56.0	5.73	6	Secondary Yolk	460	8	0
7	Cont.	0	ND	ND	ND	ND	ND	ND	0	0	Mat.	15.0	40.0	3.70	6	Secondary Yolk	460	0	0
2/19	Exp.	0.075	5.262	4.918	2.378	2.023	10.180	14.581	136X	194X	Mat.	17.0	63.0	7.63	8	Migratory Nucl.	670	10	28

[1] Tissue concentrations of other monocyclics (M2) and dicyclics measured only in mature ovaries. Mean concentrations in Table 4.

[2] GSI = Gonadosomatic Index = Ovary Wet Weight X 100/Body Wet Weight.

[3] Stages from Yamamoto, 1956.

Table 7. Means of ovarian and egg parameters showing acceleration of maturation in ovaries of exposed flounder. Mature females equally represented in control and exposed samples. Experiment 2.

						Eggs					
	No.		Ovaries			Predominant Maturation Stage			Max.	Percentage	
Treatment	Fem. (n)	Maturity	Length (cm)	Wet Wt. (g)	GSI[1]	Stage No.	Ovaries (n)	Description	Diam. (μ)	Abnormal (%)	Dead (%)
Control	3	Immature	5.1	2.5	0.30	3	3	Perinucleolus	110	0	0
Exposed	2	Immature	7.0	4.1	0.48	3	2	Perinucleolus	110	0.5	0.2
Control	8	Maturing	17.2	72.3	5.64	6	8	Secondary Yolk only	497 (410-460)	0	0
Exposed	9	Maturing	17.0	82.2	6.59	6.6 (6-8)	5	Secondary Yolk	570 (410-670)	13.0	15.0
							3	Tertiary Yolk			
							1	Migratory Nucleus			

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[1] GSI = Gonadosomatic Index = Ovary Wet Weight X 100/Body Wet Weight.

Table 8. Summary of effects observed in immature and mature starry flounder exposed to approximately 100 ppb of the WSF of Cook Inlet crude oil for 7 days. Effects marked with asterisk also observed in flounder after 7 days of depuration. A (+) indicates an elevation of effect above controls; a (-) indicates a reduction of effect below controls. Other effects not observed in controls.

	Behavior-Adult		Liver		Gonads				
Stage-Sex	Activity	VR	Total Accum.[1]	Tissue Effects	Total Accum.[1]	Water Uptake	GSI	Gonad-Gametes Effects	Gametogenesis
Mature Male	+	+	73X	+Vacuolization* +Lipid deposition* +Disruption of hepatic muralia +Sinusoidal congestion	ND	+	+	None Obvious	+Spermiation
Immature Female	+	+	12X	As above	8X	+	+	Pale color Erythrocyte Destruction Vacuolization (0.5-13.2%)* +Nuclear disintegration* +Atresia or egg death (0.2-5.5%)*	-Oocytes-atresia*
Maturing Female	+	+	135X	As above	75X	+	+	Vacuolization (3-13%) +Thicker zona radiata Egg death (5.8-15.0%)	+Egg size +Maturation rate +Vitellinogenesis
Adult Female-Resting stage (Yocom et al., manuscript)	NM	NM	2800X	NM	7X (Toluene only)	NM	NM	---------------	---------------

[1] Total Accumulation Mean Tissue Concentration of Monocyclics (M-1) and Cyclohexanes (CH)/Mean Water Concentration of M-1 and CH.

ND = Not detectable; NM Not measured; GSI = Gonadosomatic Index.

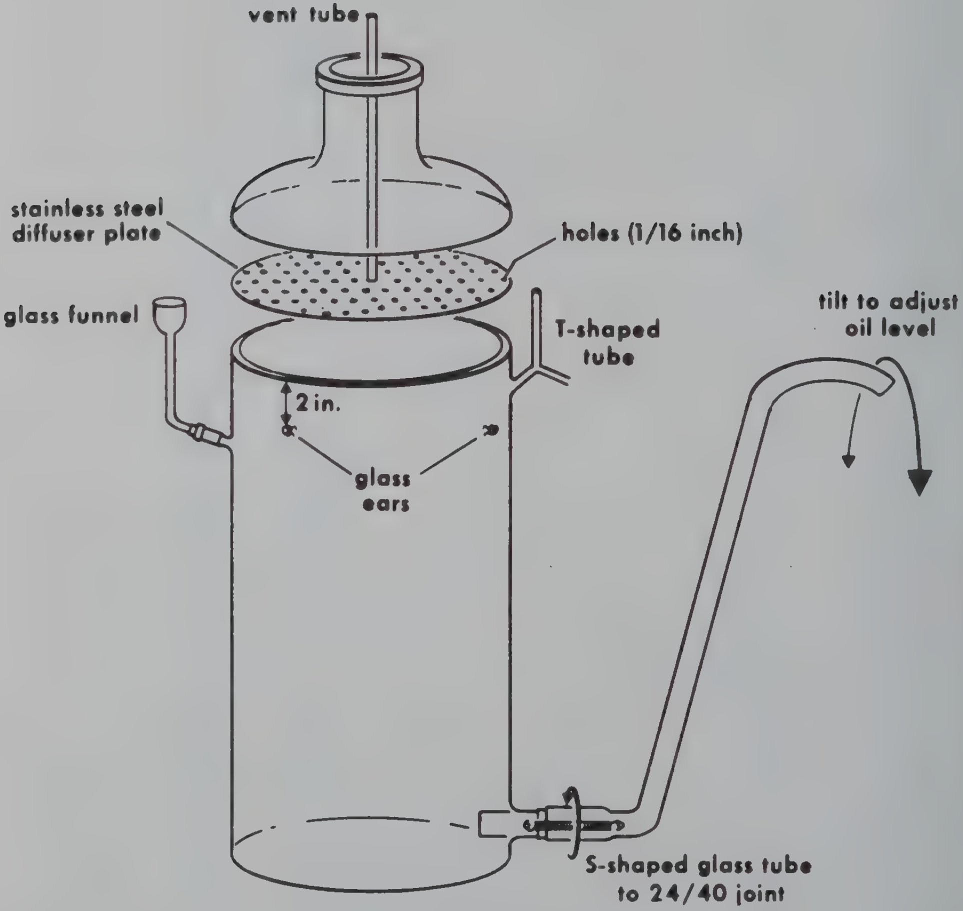
vent tube
stainless steel diffuser plate
holes (1/16 inch)
glass funnel
T-shaped tube
tilt to adjust oil level
2 in.
glass ears
S-shaped glass tube to 24/40 joint

Figure 1. Apparatus (solubilizer) for continuously dosing flounder with the water-soluble fractions (WSF) of crude oil (from Benville et al., manuscript in preparation).

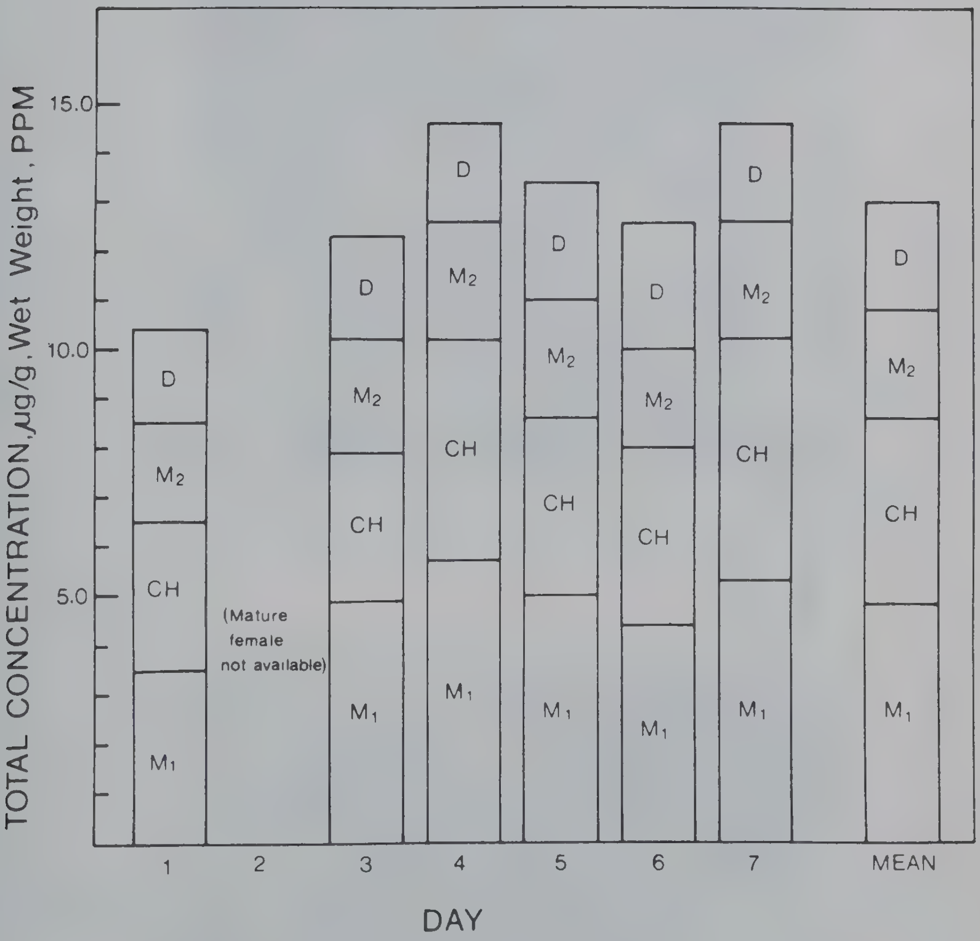

Figure 2. Concentrations of aromatics and alkyl cyclohexanes in maturing ovaries of starry flounder. M1 = Monocyclics 1; CH = Cyclohexanes; M2 = Monocyclics 2; D = Dicyclics. Mean: M1 = 37%; CH = 29%; M2 = 17%; D = 17%.

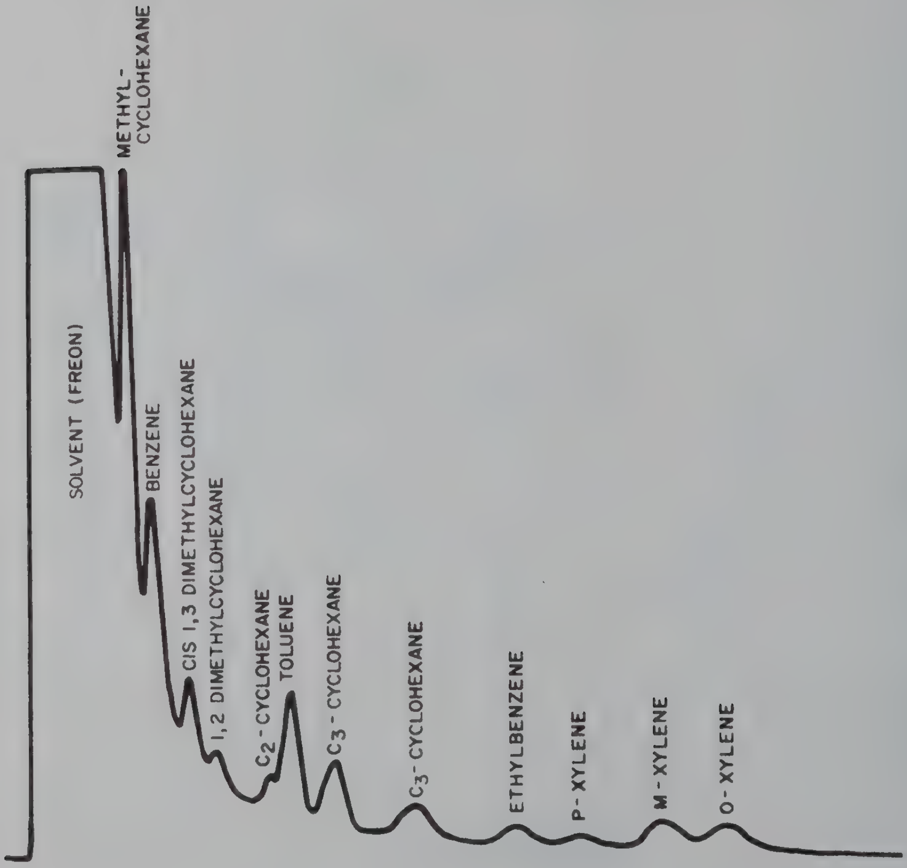

Figure 3. Chromatogram of low-boiling-point hydrocarbons detected in a maturing ovary of a starry flounder exposed to 115 ppb WSF in the water column for 7 days. Total concentration = 8.43 μg/g (ppm).

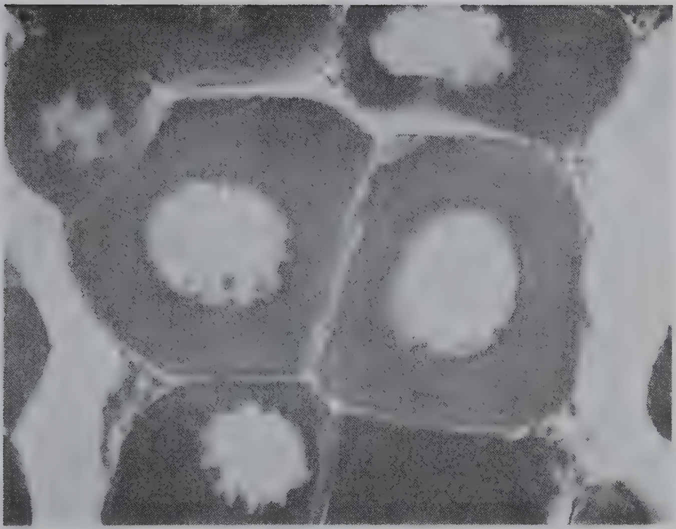

Figure 4A Photomicrograph of normal immature eggs (perinucleolus) stage in control flounder. 400 X.

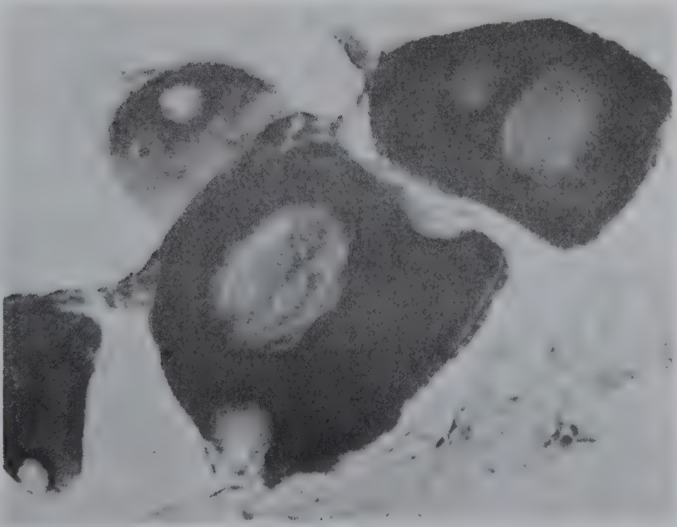

Figure 4B Photomicrograph of abnormal immature eggs (perinucleolus stage) in exposed flounder. Eggs have cytoplasmic vacuoles. 400 X.

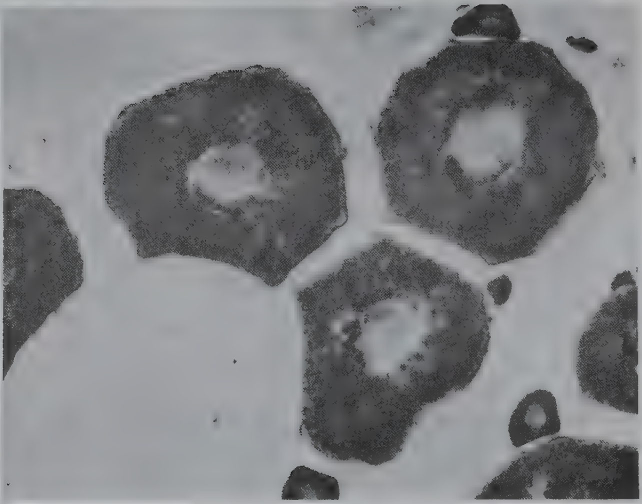

Figure 5A Photomicrograph of normal mature eggs (secondary yolk stage) in control flounder. 100 X.

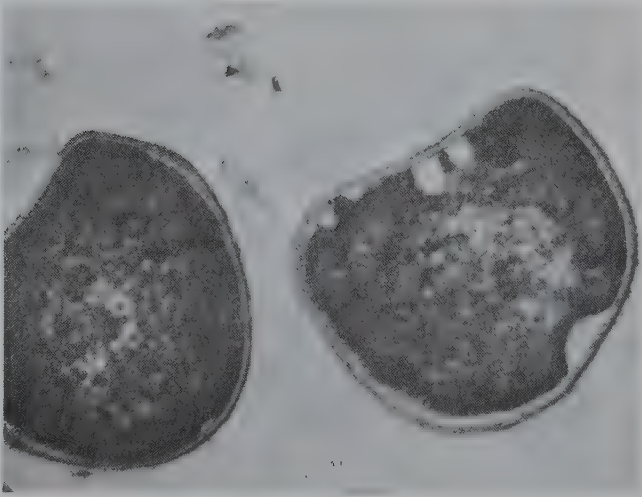

Figure 5B Photomicrograph of abnormal mature eggs (tertiary yolk stage) in exposed flounder. Eggs have cytoplasmic vacuoles. 100 X.

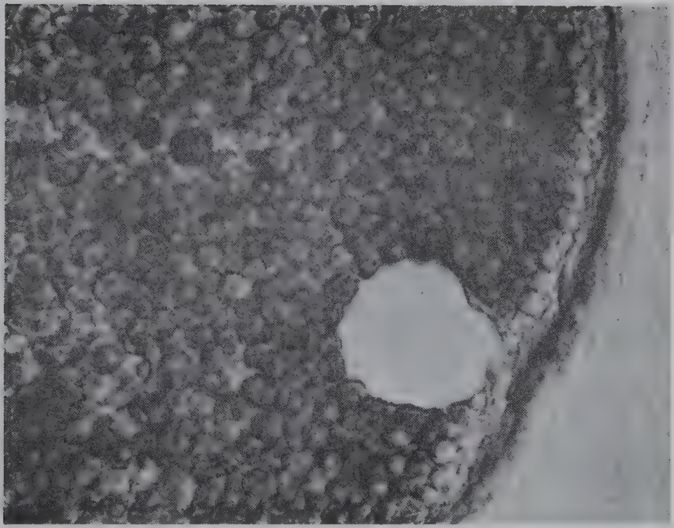

Figure 6A Photomicrograph of abnormal mature egg (tertiary yolk stage) in exposed flounder. Cytoplasmic vacuole in periphery of egg between cytoplasm and zona radiata. 400 X.

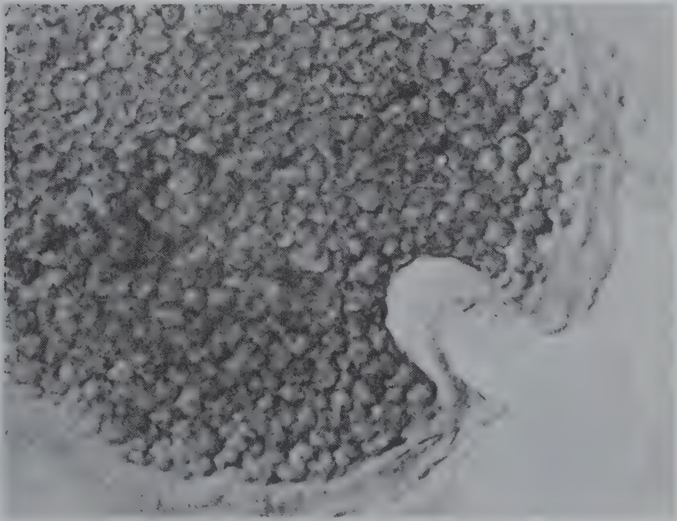

Figure 6B Photomicrograph of abnormal mature egg (tertiary yolk stage) in exposed flounder. Cytoplasmic vacuole in periphery of egg extruding through zona radiata. 400 X.

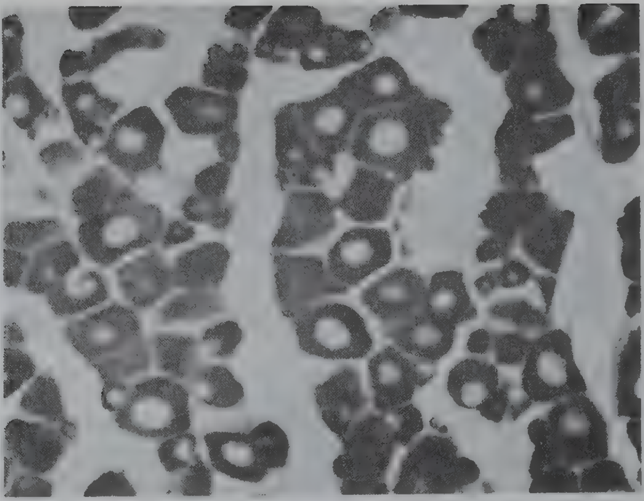

Figure 7A Photomicrograph of normal immature eggs (perinucleolus stage) in control flounder. Note compact groups of many eggs. 100 X.

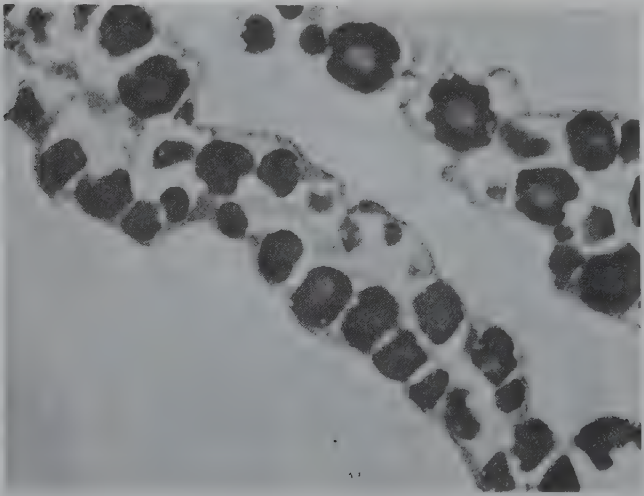

Figure 7B Photomicrograph of immature eggs in perinucleolus stage in exposed flounder. Note relatively small numbers of eggs compared to control. 100 X.

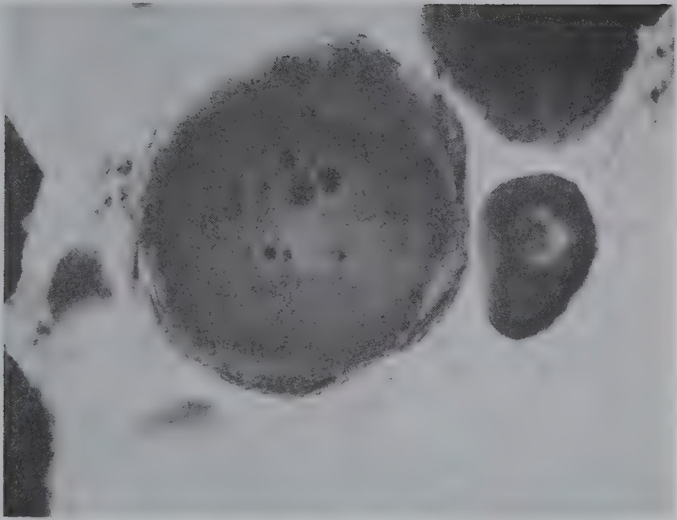

Figure 8A Photomicrograph of dying immature egg (possibly atresic) in exposed flounder. Nucleoplasm starting to coalesce into droplets. 400 X.

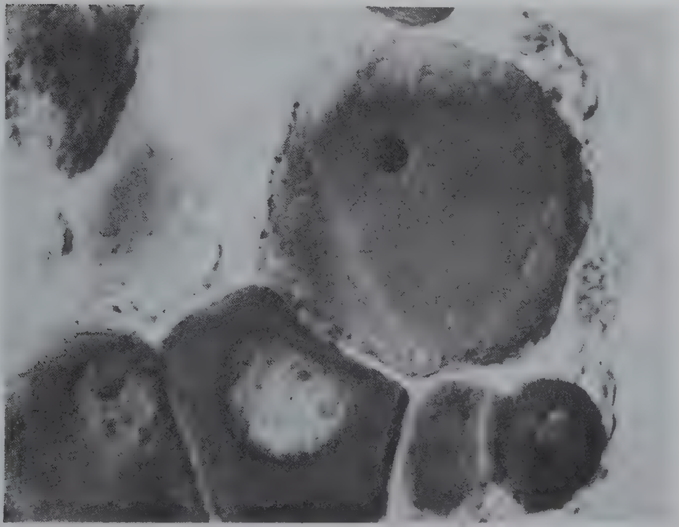

Figure 8B Photomicrograph of dying immature egg (possibly atresic) in exposed flounder. Nucleoplasm coalesced into single droplet, nuclear and cell membranes disintegrated. 400 X.

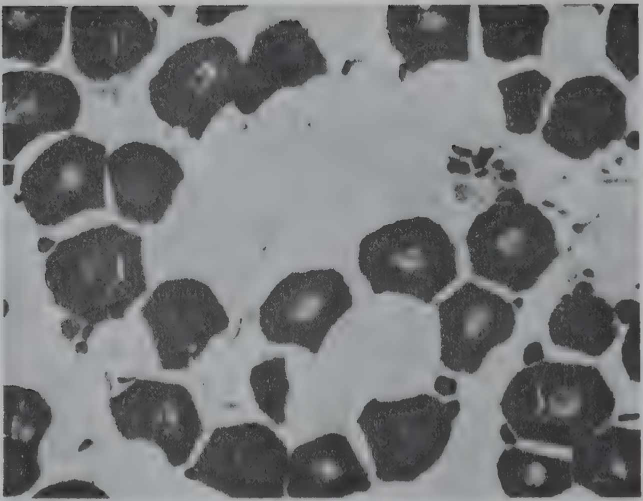

Figure 9A Photomicrograph of normal mature eggs (secondary yolk stage) in control flounder. 40 X.

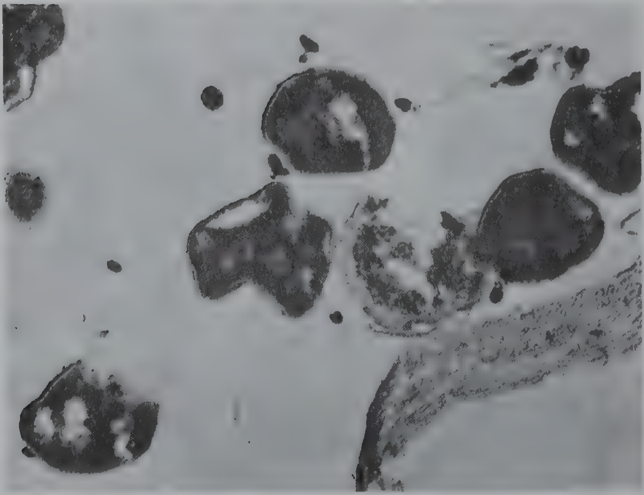

Figure 9B Photomicrograph of dying mature eggs (tertiary yolk stage) in exposed flounder. Note necrosis of eggs, thickened zona radiata. 40 X.

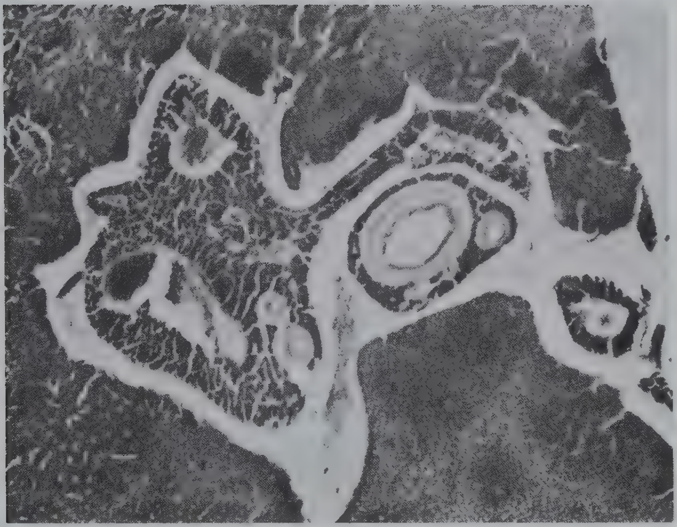

Figure 10A Section of liver tissue from control flounder. 40 X.

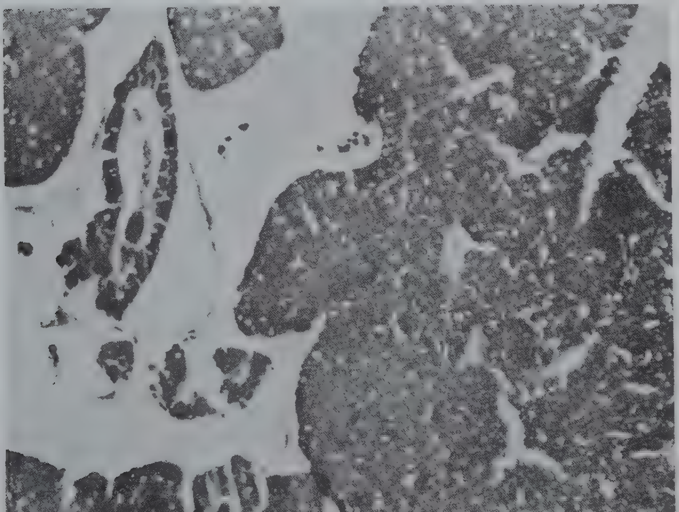

Figure 10B Section of liver tissue from exposed flounder showing heavy vacuolization. 40 X.

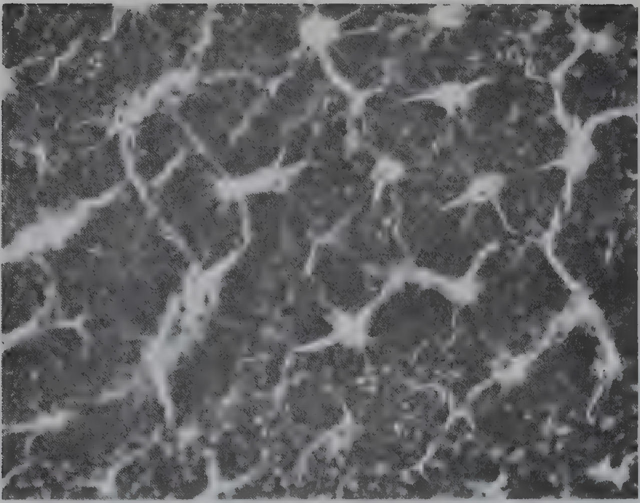

Figure 11A Cross section of hepatic muralia in liver of control flounder showing well-organized hepatocytes surrounding central sinusoids. 400 X.

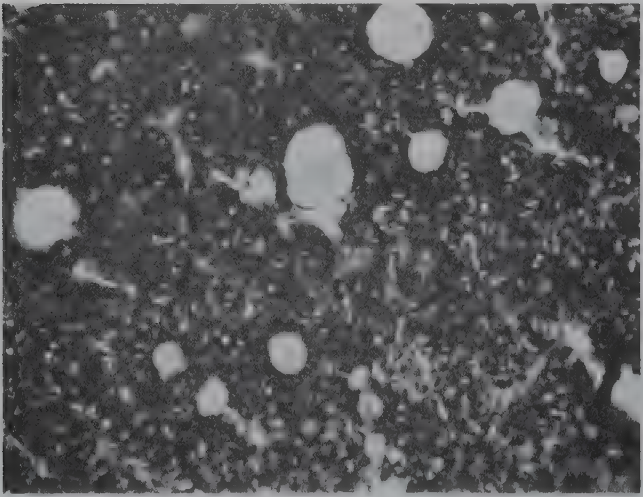

Figure 11B Cross section of hepatic muralia from liver of exposed flounder showing lack of definite structure in muralia and numerous vacuoles. 400 X.

APPENDIX

Table A. Concentrations of monocyclic aromatic components in tissues of starry flounder exposed to the WSF of Cook Inlet crude oil prior to spawning. Experiment 2. Monocyclics not detectable (<0.010 μg/g) in control flounder.

Concentration (ppm) - μg/g (wet weight)
Monocyclics 1 - (M-1)

Treatment Sample	Time (Day-Date-Hrs)	Tissue	Stage	Benzene	Toluene	Ethyl-Benzene	P-Xylene	M-Xylene	O-Xylene	Total Mono-cyclics	Total* Accumu-lation
Seawater	0-1			0.090	0.074	0.005	ND	0.007	0.006	0.182	-
Exposed #1 F	2/12	Ovary	Im-mature	0.309	ND	0.011	0.043	ND	ND	0.363	2.0X
	6	Liver		0.563	1.353	ND	ND	0.495	ND	2.411	13.2X
Exposed #2 M		Testis	Ripe	ND	ND	ND	ND	ND	ND	ND	None
		Liver		0.366	1.024	ND	ND	0.390	ND	1.780	9.8X
Seawater	1			0.046	0.060	0.004	ND	0.007	0.006	0.123	-
Exposed [illegible] F	2/13	Ovary	Mature	NM	2.734	0.426	ND	0.780	0.712	4.652	37.8X
	24	Liver		0.253	0.852	0.306	ND	0.502	ND	1.913	15.5X
Exposed #2 F		Ovary	Mature	1.633	1.873	ND	ND	ND	ND	3.506	28.5X

ND = Not detectable, but may be present.
NM = Not measured.
M = Male.
F = Female.
Mature = Maturing, but not running ripe.
Immature = Not maturing for spawning in this year.
Ripe = Males with running ripe sperm.

*Total Accumulation = Tissue Concentration (μg/g)/Water Concentration (mg/L).

Appendix - Table A (Contd)

Treatment Sample	Time (Day-Date-Hrs)	Tissue	Stage	Benzene	Toluene	Ethyl-Benzene	P-Xylene	M-Xylene	O-Xylene	Total Mono-cyclics	Total* Accumu-lation
Seawater	2			0.045	0.059	0.004	ND	0.006	0.005	0.119	-
Exposed #1 M	2/14	Testis	Ripe	ND	ND	ND	ND	ND	ND	ND	None
	48	Liver		ND	0.291	ND	ND	ND	ND	0.291	2.4X
		GB		ND	0.461	ND	ND	ND	ND	0.461	3.9X
Exposed #2 F	2/14	Ovary	Im-mature	ND	ND	ND	ND	ND	ND	ND	None
	48	Liver		ND	0.281	ND	ND	ND	ND	0.281	2.4X
		GB		ND	0.469	ND	ND	ND	ND	0.469	3.9X
Seawater	3			0.032	0.048	ND	ND	0.005	0.003	0.088	-
Exposed #1 F		Ovary	Mature	1.269	2.284	0.385	ND	0.370	0.569	4.877	55.4X
	2/15	Liver		2.820	8.334	1.740	0.726	3.922	3.262	20.804	236.4X
Exposed #2 M	72	Testis	Ripe	ND	ND	ND	ND	ND	ND	ND	None
		Liver		ND	0.524	ND	ND	ND	ND	0.524	5.9X
		GB		ND	0.442	ND	ND	ND	ND	0.442	5.0X

Appendix - Table A (Contd)

Treatment Sample	Time (Day-Date-Hrs)	Tissue	Stage	Benzene	Toluene	Ethyl-Benzene	P-Xylene	M-Xylene	O-Xylene	Total Mono-cyclics	Total* Accumu-lation
Seawater	4			0.041	0.053	0.004	ND	0.006	ND	0.104	-
Exposed #1 F	2/16	Ovary	Mature	1.554	2.846	0.400	ND	0.851	0.069	5.720	55.0X
	96	Liver		0.075	1.966	ND	ND	0.879	ND	2.920	28.1X
		GB		ND	ND	ND	ND	ND	ND	ND	None
Exposed #2 M		Testis	Ripe	ND	0.010	ND	ND	ND	ND	0.010	0.1X
		Liver		1.916	6.783	1.449	0.640	3.977	3.264	18.029	173.4X
		GB		ND	0.306	ND	ND	ND	ND	0.306	2.9X
Seawater	5			0.046	0.057	0.004	ND	0.005	ND	0.112	-
Exposed #1 F	2/17	Ovary	Mature	1.539	2.898	ND	ND	0.612	ND	5.043	45.0X
	120	Liver		0.724	1.709	0.404	ND	0.720	ND	3.557	31.8X
		GB		ND	0.348	ND	ND	ND	ND	0.348	3.1X
Exposed #2 F		Ovary	Mature	1.378	2.495	ND	ND	0.255	0.008	4.136	36.9X
		Liver		2.466	7.112	1.603	0.688	4.188	3.233	19.290	172.2X
		GB		ND	0.280	ND	ND	ND	ND	0.280	2.5X

Appendix - Table A (Contd)

Treatment Sample	Time (Day-Date-Hrs)	Tissue	Stage	Benzene	Toluene	Ethyl-Benzene	P-Xylene	M-Xylene	O-Xylene	Total Mono-cyclics	Total* Accumu-lation
Seawater	6			0.026	0.044	ND	ND	0.005	ND	0.075	-
Exposed #1 F	2/18	Ovary	Mature	NM	4.509	4.356	0.666	1.206	1.134	11.871	158.3X
Exposed #2 F		Ovary	Mature	1.254	2.290	ND	0.007	0.845	ND	4.396	58.6X
Exposed #1 F	2/19	Ovary	Mature	1.038	2.916	0.518	0.050	0.513	0.227	5.262	70.2X
Exposed #2 M		Testis	Ripe	ND	ND	ND	ND	ND	ND	ND	None
		Liver		0.995	1.974	0.594	ND	2.790	2.476	8.829	117.7X
Mean Seawater Concentrations (mg/L) (Percentages)				0.047 (41%)	0.056 (49%)	0.003 (3%)	ND (0%)	0.006 (5%)	0.003 (3%)	0.115	

APPENDIX

Table B. Concentrations of cyclohexane components in tissues of starry flounder exposed to the WSF of Cook Inlet crude oil prior to spawning. Experiment 2. Cyclohexanes and unidentified components not detectable in water column samples or control flounder.

Concentration (ppm) - μg/g (wet weight)
Cyclohexanes - (CH)

Treatment Sample	Time Day Date Hrs.	Tissue	Stage	Methyl Cyclohexane	Cis 1, 3 Dimethyl Cyclohexane	1, 2 Dimethyl Cyclohexane	Unidentified #1	Unidentified #2	C_3 Cyclohexane	Unidentified #3	Total Cyclohexanes	Maximum* Total Accumulation
Exposed #1 F	0-1 2/12 6	Ovary	Immature	ND	ND	ND	0.181	0.006	ND	ND	0.187	37X
		Liver		ND	ND	ND	ND	ND	ND	ND	ND	None
Exposed #2 M	0-1 2/12 6	Testis	Ripe	ND	ND	ND	ND	ND	ND	ND	ND	None
		Liver		ND	ND	ND	ND	ND	ND	ND	ND	None
Exposed #2 F	1 2/13 24	Ovary	Mature	1.918	ND	ND	1.078	ND	ND	ND	2.996	599X
		Liver		0.447	0.121	ND	ND	ND	ND	ND	0.568	114X
Exposed #1 M	2 2/14 48	Testis	Ripe	ND	ND	ND	ND	ND	ND	ND	ND	None
		Liver		ND	ND	ND	ND	ND	ND	ND	ND	None
Exposed #2 F	2 2/14 48	Ovary	Immature	ND	ND	ND	1.213	ND	.019	ND	1.232	246X
		Liver		ND	ND	ND	ND	ND	ND	ND	ND	None

ND = Not detectable, but may be present; M = Male; F = Female; Mature = Maturing, but not running ripe; Immature = Not maturing for spawning in this year; Ripe = Males with running ripe sperm.

*Total Accumulation = Tissue Concentration (μg/g)/Water Concentration (mg/L).
Water Concentration less than 0.010 mg/L, not detectable; estimated as 0.005 mg/L total cyclohexanes.

Appendix - Table B (Contd)

Treatment Sample	Time Day Date Hrs.	Tissue	Stage	Methyl Cyclo-hexane	Cis 1, 3 Dimethyl Cyclo-hexane	1, 2 Dimethyl Cyclo-hexane	Uniden-tified #1	Uniden-tified #2	C_3 Cyclo-hexane	Uniden-tified #3	Total Cyclo-hexanes	Maximum* Total Accumu-lation
Exposed #1 F	3 2/15 72	Ovary	Mature, not measured.									
		Liver		9.575	1.464	0.044	1.968	0.009	ND	ND	13.060	2612X
Exposed #2 M	3 2/15 72	Testis	Ripe	ND	ND	ND	ND	ND	ND	ND	ND	None
		Liver		ND	ND	ND	ND	ND	ND	ND	ND	None
Exposed #1 F	4 2/16 96	Ovary	Mature	3.255	0.603	0.287	0.383	ND	ND	ND	4.528	906X
		Liver		1.977	0.521	0.248	ND	ND	ND	ND	2.746	549X
Exposed #2 M	4 2/16 96	Testis	Ripe	ND	ND	ND	ND	ND	ND	ND	ND	None
		Liver		5.118	1.175	0.590	ND	ND	ND	ND	6.883	1377X
Exposed #1 F	5 2/17 120	Ovary	Mature	2.893	0.544	0.172	ND	ND	ND	ND	3.609	722X
		Liver		1.689	0.386	0.223	ND	ND	ND	ND	2.298	460X
Exposed #2 F	5 2/17 120	Ovary	Mature	2.446	0.419	0.158	ND	ND	ND	ND	3.023	605X
		Liver		8.286	1.727	0.671	ND	ND	ND	ND	10.684	2137X

Appendix - Table B (Contd)

Treatment Sample	Time Day Date Hrs.	Tissue	Stage	Methyl Cyclo-hexane	Cis 1, 3 Dimethyl Cyclo-hexane	1, 2 Dimethyl Cyclo-hexane	Uniden-tified #1	Uniden-tified #2	C_3 Cyclo-hexane	Uniden-tified #3	Total Cyclo-hexanes	Maximum* Total Accumu-lation
Exposed #2 F	6 2/18 144	Ovary	Mature	2.778	0.580	0.248	ND	ND	ND	ND	3.606	721X
Exposed #1 F	7 2/19 168	Ovary	Mature	2.286	0.526	0.134	1.928	ND	0.029	.015	4.918	984X
Exposed #2 M	7 2/19 168	Testis	Ripe	ND	ND	ND	ND	ND	ND	ND	ND	ND
		Liver		2.128	1.160	0.065	ND	ND	ND	ND	3.353	671X

APPENDIX

Table C. Concentrations of monocyclic and dicyclic aromatic components in mature ovaries of starry flounder exposed to WSF of Cook Inlet crude oil prior to gonadal maturation. Experiment 2. Monocyclics-2 (M-2) and dicyclics not detectable in water column samples.

Concentration (ppm) - µg/g (wet weight)[1]
Monocyclics 2 - (M-2) and Dicyclics (D)

Treatment Sample	Time Date-Day	Iso-propyl-benzene	n-propyl-benzene	Total C_3-benzenes	Total C_4-benzenes	Total[2] mono-cyclics	Naphtha-lene	2-methyl-naphtha-lene	1-methyl-naphtha-lene	Total C_2-naphtha-lenes	Total di-cyclics	Total M-2+D	Maximum[3] Total Accumu-lation
Control 1 Female	2/13 1	ND	ND	ND	ND	ND	Contami-nated	ND	ND	ND	ND	ND	None
Exposed 2 Female	2/13 1	0.109	0.138	1.307	0.423	1.977	0.691	0.813	0.272	0.127	1.903	3.880	228X
Exposed 1 Female	2/15 3	0.118	0.163	1.426	0.570	2.277	0.890	0.499	0.428	0.321	2.138	4.415	260X
Exposed 1 Female	2/16 4	0.119	0.149	1.390	0.678	2.336	0.746	0.576	0.407	0.305	2.034	4.370	257X
Exposed 1 Female	2/17 5	0.143	0.182	1.050	1.015	2.390	1.176	0.455	0.455	0.241	2.327	4.717	277X
Exposed 1 Female	2/18 6	0.116	0.155	1.222	0.516	2.009	0.788	0.679	0.489	0.598	2.554	4.563	268X
Exposed 1 Female	2/19 7	0.118	0.152	1.406	0.702	2.378	0.776	0.592	0.407	0.248	2.023	4.401	259X
Control 1 Female	2/19 7	ND	ND	.002	0.013	0.015	ND	ND	ND	ND	ND	0.015	None

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[1] Data converted from dry weight to wet weight on basis of % dry weight of total wet weight (analysis by Seattle Analytical Laboratory).

[2] Other monocyclics in Appendix Table A.

[3] Total Accumulation = Tissue Concentration (µg/g)/Water Concentration (mg/L).
Water Concentration less than 0.00025 mg/L, not detectable; estimated as 0.017 mg/L total monocyclics (M-2) and dicyclics (D).

APPENDIX

Table D. Concentration of monocyclic aromatic components in tissues of starry flounder after exposing to the WSF of Cook Inlet crude oil for 3 weeks; post-spawning period. Experiment 3. Monocyclics not detectable (<0.010 μg/g) in control flounder. Some samples pooled.

Concentration (ppm)-μg/g (wet weight)
Monocyclics-1 - (M-1)

Sample	Tissue	Stage	Benzene	Toluene	Ethyl-Benzene	P-Xylene	M-Xylene	O-Xylene	Total Mono-cyclics	Total* accumu-lation
1 Female	Ovary	Immature	ND	0.169	ND	ND	ND	ND	0.169	1.9X T
	Liver		5.011	16.272	10.435	1.283	7.057	5.524	45.582	206X
2 Male	Testis	Ripe	ND	0.352	ND	ND	ND	ND	0.352	4X T
	Liver		8.843	20.030	8.311	5.152	10.807	10.262	63.405	287X
4 Female	Ovary	Immature	ND	0.250	ND	ND	ND	ND	0.250	2.8X T
	Liver		4.049	12.332	2.731	0.939	5.869	4.641	30.561	138X
9 Male + 10 Male	Testis	Ripe	ND	0.313	ND	ND	ND	ND	0.313	3.6X T
9 Male	Liver		8.714	18.099	5.522	2.002	9.418	7.295	51.05	231X
10 Male	Liver		8.254	17.814	5.311	2.127	9.175	7.147	49.828	225X
3 Male + 11 Male	Testis	Ripe	0.359	1.002	ND	ND	ND	ND	1.361	6.2X
11 Male	Liver		15.444	30.016	8.157	2.793	12.404	9.876	78.69	356X
12 Female	Ovary	Immature	ND	0.716	ND	ND	ND	ND	0.716	8.1X T
	Liver		16.349	30.059	11.171	5.644	13.185	12.029	88.437	400X
Mean Seawater Concentration (mg/L)			0.133	0.088	ND	ND	.0003	ND	0.221	

ND = Not detectable but may be present; Immature = Ovaries in resting stage; T = Accumulation of toluene only.

*Total Accumulation = Tissue Concentration (μg/g)/Mean Water Concentration (mg/L).

APPENDIX

Table E. Concentration of cyclohexane components in tissues of starry flounder after exposing to the WSF of Cook Inlet crude oil for 3 weeks; post-spawning period. Experiment 3. Cyclohexanes not detectable (< 0.010 μg/g) in control flounder.

			Concentration (ppm)-μg/g (wet weight) Cyclohexanes - (CH)								
Sample	Tissue	Stage	Methyl cyclo-hexane	Cis 1, 3 Dimethyl cyclo-hexane	1, 2 Dimethyl cyclo-hexane	Uniden-tified #1	Uniden-tified #2	C_3 cyclo-hexane	Uniden-tified #3	Total cyclo-hexanes	Total* accumu-lation
1 Female	Ovary	Im-mature	ND	ND	ND	ND	ND	ND	ND	ND	None
	Liver		27.342	8.882	3.857	ND	1.324	ND	ND	41.405	6900X
2 Male	Testis	Ripe	0.284	ND	ND	ND	ND	ND	ND	0.284	47X
	Liver		38.471	8.455	3.803	0.463	1.310	ND	ND	52.502	8750X
4 Female	Ovary	Im-mature	0.134	ND	ND	ND	ND	ND	ND	0.134	22X
	Liver		21.615	5.729	2.578	ND	ND	ND	ND	29.922	4987X
9 Male + 10 Male	Testis	Ripe	0.312	ND	ND	ND	ND	ND	ND	0.312	52X
9 Male	Liver		35.867	7.506	3.541	0.029	0.930	ND	ND	47.873	7979X
10 Male	Liver		33.836	6.792	3.011	0.313	ND	ND	ND	43.952	7325X
11 Male + 3 Male	Testis	Ripe	0.384	ND	ND	ND	ND	ND	ND	0.384	64X
11 Male	Liver		31.744	6.842	3.143	0.561	ND	ND	ND	42.290	7048X
12 Female	Ovary	Im-mature	ND	ND	ND	ND	ND	ND	ND	ND	None
	Liver		31.984	6.863	3.057	0.368				42.272	7045X
Mean Seawater Concentration (mg/L)			ND - 0.006	ND	ND	ND	ND	ND	ND	Max. = 0.006	

ND = Not detectable but may be present. Immature = Ovaries in resting stage.

*Total Accumulation = Tissue Concentration (μg/g)/Maximum water concentration (mg/L).

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